

THE GENUS ENNEAPOGON DESV. EX P. BEAUV. (POACEAE) IN AUSTRALIA.

BY

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DECLARATION OF ORIGINALITY

The work contained in this thesis is my own, except where due acknowledgement is made, and it has not been previously submitted for a degree or diploma in any University. In particular, to the best of my knowledge it does not include any material previously published by another person except where due reference is made in the text.

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NOTE

I recognize that botanical convention normally requires the underlining or italicization of generic and species names. However, this convention was not followed in this thesis due to the lack of such facilities in the computer word processor that was used in the generation of the script.

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SUMMARY

The thesis is presented in three main parts. The first part deals with anatomy of the leaf blades; the second part deals with cytology; while the third part is concerned with a revision of the Australian members of *Enneapogon* based on gross morphology.

In the first part the epidermal and the internal anatomy are considered. The species are similar in many respects. They display a range of characters found in major sub-families of Poaceae. The species have remained conservative in some respects but have become advanced in others to adapt themselves to the harsh environment in which they grow. The implications of this are discussed.

In the second part, the chromosome numbers are reported for the first time for 11 species. The results show that they are a homogeneous group with a diploid number of $2n = 20$. The implications of the diploid nature of the species are discussed.

The third part deals firstly with axillary cleistogamy which occurs in three species, namely *E. asperatus*, *E. caerulescens*, and *E. cylindricus*. Secondly, the Australian members of *Enneapogon* Desv. ex P. Beauv. are here revised. The DELTA computer system was used in the presentation of the revision for the species. Characters used in the key and the description of the species are discussed. Twenty species are recognised. Four of these, namely *E. decipiens*, *E. conicus*, *E. eremophilus*, and *E. truncatus*, are described as new. Four varieties are recognised. Three of these, namely *E. caerulescens* var. *occidentalis*, *E. polyphyllus* var. *denudatus*, *E. oblongus* var. *papposus* are described as new, while *E. clelandii* N. Burb. is reduced to

> varietal status as *E. conicus* var. *clelandii*. Specific relationships and nomenclatural aspects are discussed under each species where warranted. Distribution and ecological information are given for each taxon described. The distribution of each species was mapped. The results show that the species, with a few exceptions, occur in the drier areas of the Australian interior. Natural hybrids recognised on the basis of morphological characters are also described.

>

1. GENERAL INTRODUCTION

Enneapogon Desv. ex P. Beauv. is a tropical, sub-tropical and arid zone genus belonging to the tribe Pappophoreae. It is the largest genus in the tribe and comprises about 30 species. Of these species 20 occur in Australia, one in North America and Central America, and the remainder in Africa and Asia. The genus is the only one of the tribe Pappophoreae to occur in Australia and the majority of the species are endemic to the continent with only 2 extending into New Guinea. Within the Australian region the species are mainly Eremaean in distribution, in a zone characterized by extreme variability of rainfall both annually and seasonally.

Historically the generic position posed problems dating from the work of Robert Brown (1810) to the end of the nineteenth century (Burbidge 1941). However, the genus is now distinguished from the other members of the tribe by the nature of its 9-awned lemmas. Reeder (1965) discussed tribal relationships and detailed the differences and similarities between the genera based on morphology, anatomy of the leaf, and embryology.

While the generic boundaries currently pose no problems, members of the genus Enneapogon are extremely closely related and not readily distinguished from each other and therefore have been a source of difficulty to botanists who deal with them. Previous authors based their work on characters such as habit, awn length, and indumentum of the lemmas and the culms to distinguish the species. A careful study of the Australian material has shown that these characters are variable and not sufficiently reliable to merit their use. Bentham (1878) used the length of the outer glume and the number of nerves but

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he, too, encountered a number of problems. The last revision of the Australian members of Enneapogon was by Burbidge (1941) in which 19 species were recognised. She contemplated a future revision as adequate material was not available to her at the time.

It was initially envisaged that the present revision of the Australian Enneapogon species would entail a taxonomic study based chiefly on gross morphology. The existence of discontinuity was used as the main species criterion. The Australian members of Enneapogon are also poorly known anatomically and cytologically. To supplement the taxonomic revision based on gross morphology, anatomical studies of the leaf blades were carried out, and cytological studies involving chromosome counts were made for some species. In the light of morphological, anatomical, and cytological information an attempt was made to gain an understanding of the relationships exhibited by the species.

2. ANATOMY: LEAF BLADE

2.1. INTRODUCTION

Often, anatomical considerations are beyond the scope of many who want to identify grasses and therefore are separated here from morphological considerations. However, taxonomists have realised the importance of anatomical features for systematic purposes as early as the end of the last century and it has gained momentum in recent years.

Leaf anatomy, as revealed by transverse sections, has been emphasized as fundamental evidence in grass taxonomy (e.g. Avdulov 1931, Prat 1936, Hubbard 1948, Tateoka 1956d). Duval-Jouve (1875) was the first to attempt its use for systematics. Avdulov (1931) recognised 2 types, I and II, based on the distribution of chloroplasts in the leaf. Later Prat (1936) recognised 2 major types, the panicoid and the festucoid, which almost correspond to those of Avdulov. In addition Prat found that the panicoid type can be classified into 2 subtypes, the eupanicoid and the chloridoid, based on the type of microhairs and the silica cells. Prat suggested the system of eupanicoides and chloridoides under sub-family Panicoideae. In essence these two types were accepted as basic by subsequent authors (e.g. Vickery 1935, Burbidge 1946, Tateoka 1956a, b, c, d) until Stebbins (1956) illustrated four types of leaf anatomy, adding the bambusoid and the chloridoid to the panicoid and the festucoid of Avdulov and Prat. Anatomy of grass systematics has been studied more recently by various investigations. Brown (1958) expressed the opinion

>
that grasses should be divided into 6 major groups according to leaf anatomy.

On the other hand, epidermal cuticles are more resistant to the process of digestion and decay and leaf epidermal data can be gathered from, e.g., animal gut contents and faeces (Davies 1956). Metcalfe (1954) pointed out that certain characters of the leaf epidermis such as the shape of subsidiary cells of the stomata, as well as the microhairs and silica cells, are systematically important.

Concerning the tribe Pappophoreae, to which the genus *Enneapogon* belongs, the works of Duval-Jouve (1875), Lohaus (1905), Sabnis (1921), Prat (1936), Chippindall (1955), Tateoka et al. (1959), Metcalfe (1960), Stebbins & Crampton (1961), Jacques-Felix (1962), Stewart (1964), Reeder (1965), Watson & Dallwitz (1980) have contributed greatly to a knowledge of the internal anatomy and leaf epidermal characters, and also provide a source of many of the descriptive terms.

Lohaus (1905) initiated the work on leaf anatomy and epidermal features in Australian members of *Enneapogon*. Chase (1946) pointed out that actually the plant which Lohaus studied was a species of *Enneapogon* since the genus *Pappophorum* is confined to the Americas. A note under *P. commune* F. Muell. in Chase & Niles (1962) states:

"A group name for all Australian species, the 4 of R. Br., 3 of Lindley, and *P. coerulescens* Gaud. = *Enneapogon*."

Prat (1935) studied representatives of *Pappophorum* and *Cottea* and was impressed with the elongate stalked-glandular hairs. He indicated that they were similar to those of Lohaus (1905) in *P. commune* F. Muell. Chippindall (1955), referring to the Pappophoreae, noted that many

members of the tribe were characterized by the stalked-glandular hairs that occurred on the vegetative, as well as the floral, parts.

2.2. MATERIALS AND METHODS

2.2.1. ABAXIAL EPIDERMIS

All material used was obtained from dried herbarium specimens. The lower epidermis of the leaves from the middle of the culms was used throughout the preparations. The lower epidermis is easy to handle and presents fewer problems of irregularities in ribbing and cell size (Clifford & Watson 1977). The dried leaves were gently boiled in water with 3 to 5 drops of Teepol until sufficiently softened to cut by hand. They were then washed in water and fixed in 70% alcohol, in which they were stored until required. Pieces about 1 cm long were obtained from the middle of the leaf blades. Under a binocular microscope, the upper epidermis was slightly damaged with a razor, which allowed penetration of the bleach (sodium hypochlorite). The pieces were discoloured and softened further in the bleach (10 minutes), then rinsed in distilled water. Care was taken to remove much of the bleach from the pieces. Under a binocular microscope the unwanted tissue was scraped off, leaving the lower epidermis. The staining schedule of Purvis et al. (1966) was used throughout this study, but with some minor modifications. The pieces were stained in phenol bismark brown (10 to 20 minutes), rinsed in tap water (3 minutes), then in distilled water (3 minutes). They were dehydrated

through 70% alcohol (10 to 20 minutes), rinsed in two changes of absolute alcohol (3 minutes each) and cleared in xylene. They were mounted in Depex with the outer surface of the lower epidermal strip uppermost on the slide.

A micrometer was used for the measurement of length and width, and the mean of 100 was adopted as the standard for each type of measurement, e.g., microhair length, stomata width, etc.

2.2.2. TRANSVERSE SECTION OF LEAF BLADE

Pieces from the middle of the leaf were hand-sectioned, stained and mounted for microscopic examination as above.

2.3. GENERIC DESCRIPTION

2.3.1. ABAXIAL EPIDERMIS

2.3.1.1. COSTAL ZONE

The costal zone consists of short cells in long rows alternating with silica cells. Rows lacking short cells and silica cells alternate with those having them. Silica cells are mostly cross-shaped to dumbbell-shaped, or rarely nodular. Large prickles are present, often turned upwards (Plate 1).

2.3.1.2. INTERCOSTAL ZONE

The intercostal zone consists of 4 to 8 rows of long cells with sinuous walls. Hairs of two types occur in this zone: simple and bicellular stalked-glandular. Two types of short cells also occur in this zone: the hemispherical cells associated with hair bases, and the variously shaped cells that occur at random. Prickles smaller than those over the costal zone, and pronounced spicules on leaf margins, are often present. Two rows of stomata, rarely 1 or 3, with triangular to tall, dome-shaped subsidiary cells occur in this zone (Plate 1).

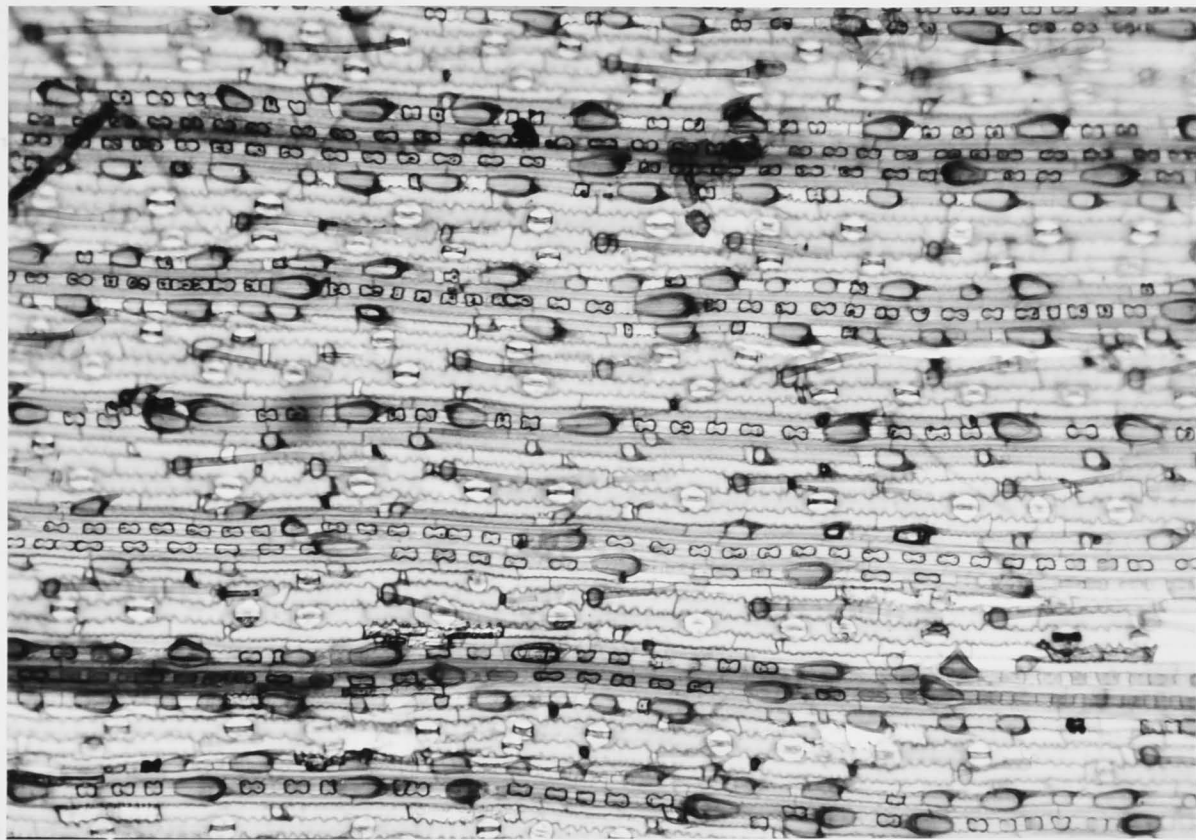


Plate 1: Abaxial leaf epidermis of *E. virens*, x200. Dumbbell silica cells over the costal zone; stalked glandular microhairs with hemispherical short cells at the base.

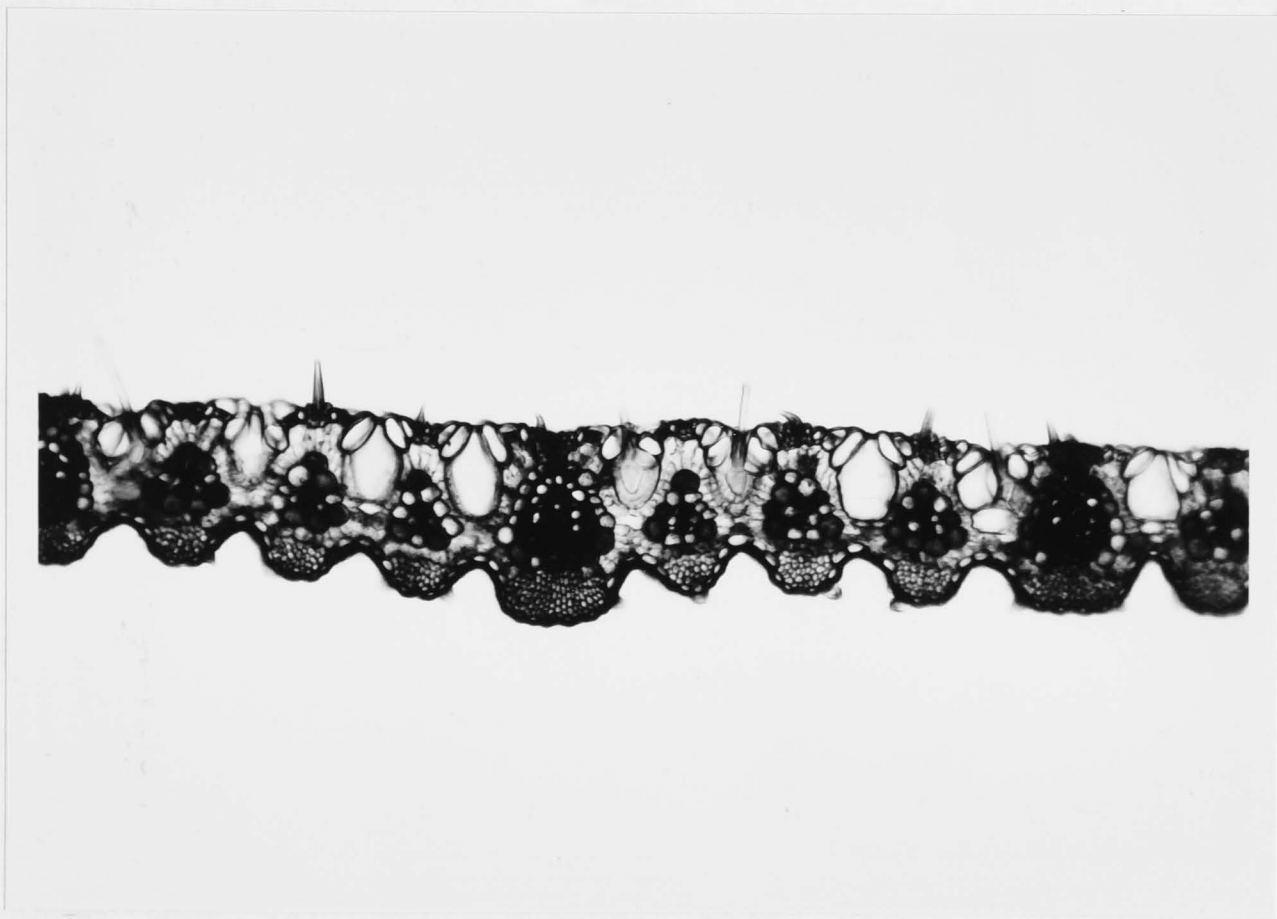


Plate 2: T. S of *E. caerulescens*, x40. Prominent abaxial ribs; triangular outer bundle sheaths with large cells at the corners.

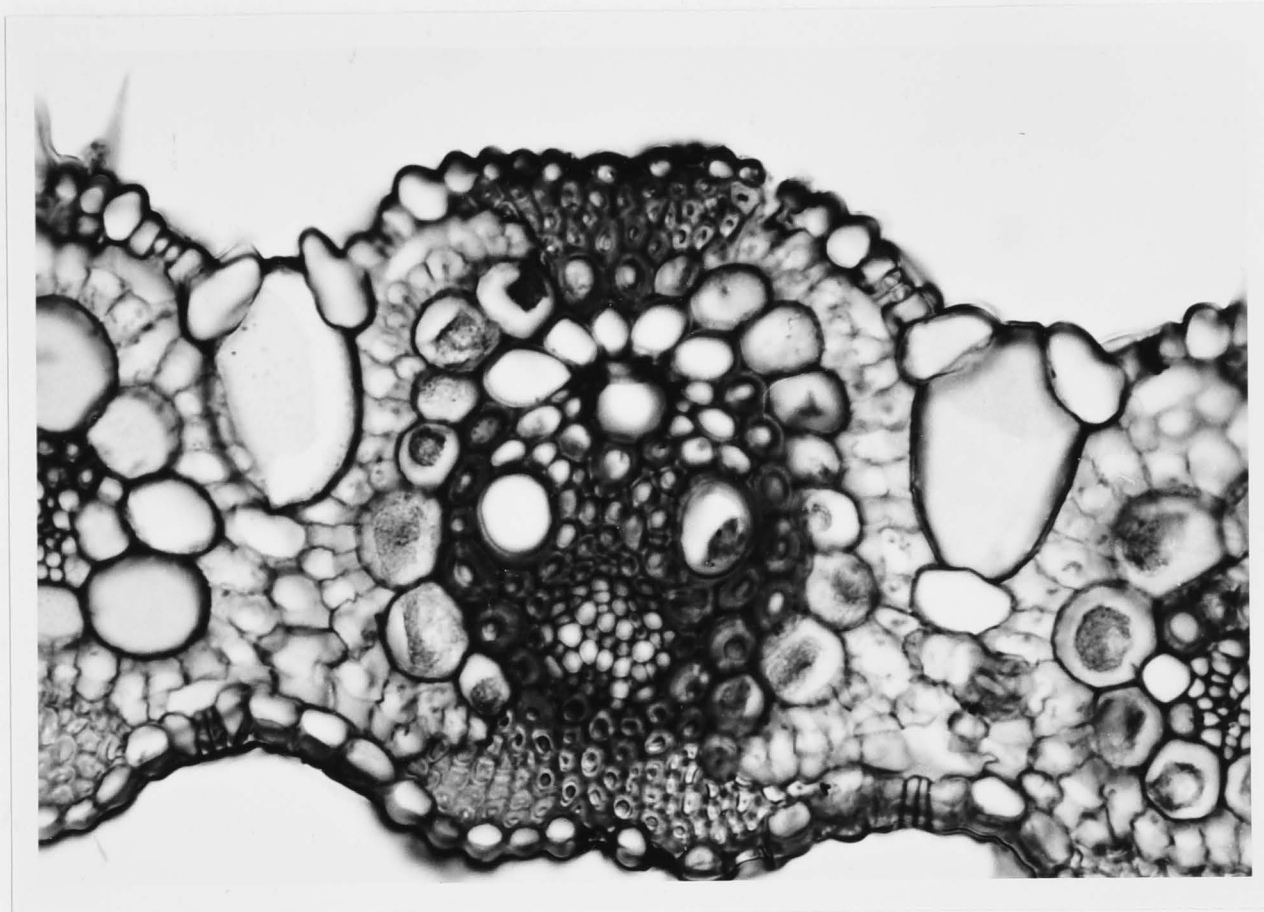


Plate 3: T. S of *E. conicus*, x 400. Vascular bundle with an inner sheath of thickened cell walls especially abaxially; mesophyll of radiate chlorenchyma; colourless cells traversing the mesophyll.

2.3.2. TRANSVERSE SECTION OF LEAF BLADE

In outline (Plates 2 & 3) the leaves are more or less nodular with shallow furrows separating ribs. The midrib consists of one vascular bundle and it is not easily distinguished from other main ribs in transverse sections. Vascular bundles are mostly small, crowded and variously shaped; large vascular bundles are generally circular in outline.

Depending on the size of the vascular bundles and upon the species, the sclerenchyma was found in variable amounts beneath the

adaxial epidermis and above the abaxial epidermis. All sclerenchyma of the leaf (excluding any at the leaf margins) is associated with vascular bundles. At least some vascular bundles have adaxial girders, and some are accompanied by strands. The combined adaxial and abaxial girders over the main vascular bundles form I- to T-shaped anchors. The mesophyll tissue consists of radiate chlorenchyma around vascular bundles, with a maximum cells-distant count of less than 4. [The maximum cells-distant count is the number of chlorenchymatous mesophyll cells between laterally-adjacent leaf veins in transverse section, excluding traversing colourless cells (Clifford & Watson 1977).]

Bundle sheaths are conspicuously double around main vascular bundles. The inner sheath of thick-walled cells and the outer of large parenchyma cells are present. A continuous outer sheath is obvious in small vascular bundles; the sheath is more or less angular in outline. The outer sheath cells have a diameter ranging from 12 to 30 micrometres, and a dark green in contrast to the mesophyll chlorenchyma cells. Cells of individual sheaths are more or less constant in size. The outer sheath is commonly interrupted abaxially by sclerenchyma tissue.

The inner sheath cells are especially thickened on the inner tangential and radial sides. There is a transition of cell size from adaxial to abaxial end. The adaxial cells are often larger than those on the abaxial end, a transition which seems to go hand-in-hand with the diameter of the lumen of these cells, that is, the lumen is large adaxially and progressively decreases abaxially.

Bulliform cells are in fan-shaped groups. The central large cell is accompanied by 1 to 4 elliptic cells on either side.

Colourless cells are associated with the bulliforms. The colourless cells penetrate the mesophyll and commonly traverse the mesophyll from adaxial to abaxial epidermis. Hairs occur on either surface; hair bases are sunken within the region of the central bulliform cells or opposite them.

Stomata occur on either surface, each with an air space below. Air spaces between the mesophyll chlorenchyma are absent.

2.4. DESCRIPTION OF THE SPECIES

2.4.1. *E. avenaceus* (Lindl.) C. E. Hubb.

5 to 8 rows of long cells between the costal zones. Long cells 13 to 174 micrometres long (average 77.7); 10 to 26 micrometres wide (average 17.4). 1 short cell associated with each hair base. 1 to 2 rows of stomata between the costal zones. Stomata 18.2 to 31.2 micrometres long (average 23.2); 15.6 to 22.1 micrometres wide (average 19.2). Prickles associated with the costal zone 32.5 to 117 micrometres long (average 63); absent from the central portion of the costal zone. Costal zone 10.4 to 91 micrometres wide (average 48.3). Silica cells 10.4 to 31.2 micrometres long (average 20.4); dumbbell-shaped to nodular. Microhairs 56.6 to 150.8 micrometres long (average 112.2).

Leaf blade in transverse section nodular (adaxial surface more or less flat). Abaxial ribs irregular in size; main ribs flattened in outline. Mesophyll chlorenchyma distinctively radiate.

Maximum cells-distant count of 1 to 2 (rarely 3). Inner sheath incomplete in large vascular bundles; conspicuous in small vascular bundles. Outer sheath interrupted adaxially and abaxially; cells of individual sheaths constant in size; outline of individual sheaths angular in small vascular bundles (circular towards margins). Colourless cells rarely traversing the mesophyll. Combined adaxial and abaxial girders T-shaped. Strands 1 to 6 cells high (present on adaxial or abaxial ends).

Voucher specimens for anatomical study: Lazarides 4354 (CANB), Moore 5806 (CANB), and Forde 378 (CANB).

2.4.2. *E. virens* (Lindl.) Kakudidi

5 rows of long cells between the costal zones. Long cells 15.6 to 122 micrometres long (average 73.6); 13 to 23.5 micrometres wide (average 16.9). 1 short cell associated with each hair base. 1 to 2 rows of stomata between the costal zones. Stomata 18.2 to 26 micrometres long (average 21.5); 15.6 to 24.7 micrometres wide (average 19.8). Prickles associated with the costal zone 31.2 to 67.6 micrometres long (average 49); absent from the central portion of the costal zone. Costal zone 26 to 70.2 micrometres wide (average 42.1). Silica cells 15 to 28.6 micrometres long (average 21.5); cross-shaped to dumbbell-shaped, or nodular (rare). Microhairs 23.4 to 176.8 micrometres long (average 95.3).

Leaf blade in transverse section nodular (abaxial ribs more prominent). Adaxial ribs irregular in size. Abaxial ribs irregular in size; main ribs flattened in outline. Mesophyll chlorenchyma

distinctively radiate. Maximum cells-distant count of 1 (rarely 2). Inner sheath complete in large vascular bundles (not clearly defined abaxially); conspicuous in small vascular bundles. Outer sheath interrupted adaxially and abaxially; cells of individual sheaths constant in size; outline of individual sheaths angular in small vascular bundles. Colourless cells commonly traversing the mesophyll. Combined adaxial and abaxial girders I-shaped. Strands 1 to 5 cells high (present on adaxial and or abaxial ends).

Voucher specimens for anatomical study: Adams 1176 (CANB), Mitchell s.n 1846 (CGE), and Moore 7631 (CANB).

2.4.3. *E. gracilis* (R. Br.) P. Beauv.

4 to 5 rows of long cells between the costal zones. Long cells 18.2 to 161.2 micrometres long (average 94.6); 13 to 26 micrometres wide (average 18.8). 1 short cell associated with each hair base. 1 to 2 rows of stomata between the costal zones. Stomata 20.8 to 31.2 micrometres long (average 24.9); 18.2 to 26 micrometres wide (average 23). Prickles associated with the costal zone 26 to 57.8 micrometres long (average 40.6); present on the central portion of the costal zone. Costal zone 26 to 104 micrometres wide (average 59.4). Silica cells 14.3 to 36.4 micrometres long (average 22.3); cross-shaped to dumbbell-shaped. Microhairs 52 to 254 micrometres long (average 112.5).

Leaf blade in transverse section with prominent abaxial ribs only (with shallow furrows separating the ribs). Abaxial ribs irregular in size; main ribs flattened in outline. Mesophyll

chlorenchyma distinctively radiate. Maximum cells-distant count of 1 (rarely 2). Inner sheath complete in large vascular bundles; conspicuous in small vascular bundles. Outer sheath interrupted adaxially; cells of individual sheaths constant in size; outline of individual sheaths angular in small vascular bundles (markedly so with slightly larger cells at abaxial corners). Colourless cells commonly traversing the mesophyll. Combined adaxial and abaxial girders I-shaped. Strands 2 to 5 cells high (present on abaxial or both ends). Voucher specimens for anatomical study: Adams 1071 (CANB), and Hubbard & Winders 7545 (CANB).

2.4.4. *E. eremophilus* Kakudidi

5 to 6 rows of long cells between the costal zones. Long cells 15.6 to 104 micrometres long (average 63.3); 11.7 to 20.8 micrometres wide (average 17.2). 1 short cell associated with each hair base. 2 rows of stomata between the costal zones. Stomata 18.2 to 27.3 micrometres long (average 23.7); 14.3 to 22.1 micrometres wide (average 18). Prickles associated with the costal zone 26 to 78 micrometres long (average 50.6); absent from the central portion of the costal zone. Costal zone 26 to 98.8 micrometres wide (average 51.1). Silica cells 14.3 to 26 micrometres long (average 20.2); cross-shaped to dumbbell-shaped, or nodular (rare). Microhairs 74.4 to 130 micrometres long (average 102.4).

Leaf blade in transverse section with prominent abaxial ribs only. Abaxial ribs irregular in size; main ribs flattened in outline. Mesophyll chlorenchyma distinctively radiate. Maximum cells-distant

count of 1. Inner sheath complete in large vascular bundles; conspicuous in small vascular bundles. Outer sheath interrupted adaxially and abaxially; cells of individual sheaths constant in size; outline of individual sheaths circular in small vascular bundles. Colourless cells commonly traversing the mesophyll. Combined adaxial and abaxial girders T-shaped. Strands 2 to 6 cells high (present on adaxial or abaxial end).

Voucher specimens for anatomical study: Latz 4447 (CANB) and Perry 986 (CANB).

2.4.5. *E. purpurascens* (R. Br.) P. Beauv.

5 to 7 rows of long cells between the costal zones. Long cells 37.7 to 152.1 micrometres long (average 95.2); 13 to 26 micrometres wide (average 18.9). 1 short cell associated with each hair base. 2 rows of stomata between the costal zones. Stomata 20.8 to 31.2 micrometres long (average 25.9); 15.6 to 22.1 micrometres wide (average 18.7). Prickles associated with the costal zone 36.4 to 85.8 micrometres long (average 56.7); absent from the central portion of the costal zone. Costal zone 36.4 to 91 micrometres wide (average 63.3). Silica cells 10.4 to 29 micrometres long (average 21.8); dumbbell-shaped to nodular. Microhairs 41.4 to 241 micrometres long (average 146.5).

Leaf blade in transverse section nodular. Adaxial ribs irregular in size. Abaxial ribs irregular in size; main ribs flattened in outline. Mesophyll chlorenchyma distinctively radiate. Maximum cells-distant count of 1. Inner sheath complete in large vascular

bundles; conspicuous in small vascular bundles. Outer sheath interrupted adaxially and abaxially; cells of individual sheaths constant in size; outline of individual sheaths angular or circular in small vascular bundles. Colourless cells commonly traversing the mesophyll. Combined adaxial and abaxial girders T-shaped. Strands 2 to 4 cells high (present on both adaxial and abaxial ends).

Voucher specimens for anatomical study: Lazarides 6307 (CANB), Bedbrook 6B (PERTH) and Ganley s.n CANB 144149 (CANB).

2.4.6. *E. decipiens* Kakudidi

5 to 6 rows of long cells between the costal zones. Long cells 18.2 to 117 micrometres long (average 80.4); 14.3 to 24.7 micrometres wide (average 19.4). 1 short cell associated with each hair base. 2 rows of stomata between the costal zones. Stomata 18.2 to 26 micrometres long (average 22.5); 14.3 to 19.5 micrometres wide (average 17.2). Prickles associated with the costal zone 23.5 to 58.8 micrometres long (average 45.2); absent from the central portion of the costal zone. Costal zone 21.1 to 144.4 micrometres wide (average 56.5). Silica cells 10.4 to 31.2 micrometres long (average 27.8); cross-shaped to dumbbell-shaped. Microhairs 93.6 to 176.8 micrometres long (average 127.1).

Leaf blade in transverse section nodular. Adaxial ribs irregular in size. Abaxial ribs constant in size; main ribs flattened in outline. Mesophyll chlorenchyma distinctively radiate. Maximum cells-distant count of 1 (rarely 2). Inner sheath complete in large vascular bundles; conspicuous in small vascular bundles. Outer sheath

interrupted abaxially; cells of individual sheaths constant in size; outline of individual sheaths angular in small vascular bundles. Colourless cells commonly traversing the mesophyll. Combined adaxial and abaxial girders I-shaped. Strands 1 to 3 cells high (common on adaxial end).

Voucher specimens for anatomical study: Wilson 53 (CANB) and Must 409 (CANB).

2.4.7. *E. pallidus* (R. Br.) P. Beauv.

5 to 6 rows of long cells between the costal zones. Long cells 26 to 117 micrometres long (average 79.1); 18.2 to 32.5 micrometres wide (average 24.6). 1 short cell associated with each hair base. 2 rows of stomata between the costal zones. Stomata 26 to 37.7 micrometres long (average 31.3); 20.8 to 29.9 micrometres wide (average 25.3). Prickles associated with the costal zone 28.6 to 59.8 micrometres long (average 43.3); absent from the central portion of the costal zone. Costal zone 28.6 to 156 micrometres wide (average 62.2). Silica cells 16.9 to 29.9 micrometres long (average 21.5); dumbbell-shaped to nodular. Microhairs 46.8 to 70 micrometres long (average 54.6).

Leaf blade in transverse section nodular. Adaxial ribs irregular in size. Abaxial ribs irregular in size; main ribs flattened in outline. Mesophyll chlorenchyma distinctively radiate. Maximum cells-distant count of 1. Inner sheath complete in large vascular bundles; conspicuous in small vascular bundles. Outer sheath interrupted adaxially and abaxially; cells of individual sheaths

constant in size; outline of individual sheaths angular in small vascular bundles. Colourless cells commonly traversing the mesophyll. Combined adaxial and abaxial girders T-shaped. Strands 3 to 11 cells high (common on abaxial end).

Voucher specimens for anatomical study: Specht 653 (CANB) and Latz 1475 (CANB).

2.4.8. *E. oblongus* N. Burb.

5 to 6 rows of long cells between the costal zones. Long cells 23.4 to 158.4 micrometres long (average 82); 13 to 24.7 micrometres wide (average 18.5). 1 short cell associated with each hair base. 2 rows of stomata between the costal zones. Stomata 20.8 to 28.6 micrometres long (average 25.4); 14.5 to 26 micrometres wide (average 20.3). Prickles associated with the costal zone 31.2 to 93.6 micrometres long (average 54.6); absent from the central portion of the costal zone. Costal zone 13 to 85.6 micrometres wide (average 50.3). Silica cells 14.3 to 27.3 micrometres long (average 20); cross-shaped to dumbbell-shaped. Microhairs 41.6 to 130 micrometres long (average 53.4).

Leaf blade in transverse section nodular. Adaxial ribs constant in size. Abaxial ribs constant in size; all rounded in outline. Mesophyll chlorenchyma distinctively radiate. Maximum cells-distant count of 2. Inner sheath complete in large vascular bundles; inconspicuous in small vascular bundles. Outer sheath interrupted adaxially and abaxially; cells of individual sheaths constant in size; outline of individual sheaths circular in small

vascular bundles. Colourless cells commonly traversing the mesophyll. Combined adaxial and abaxial girders I-shaped. Strands 1 to 5 cells high (present on adaxial, abaxial or both end).

Voucher specimens for anatomical study: Perry 3296 (CANB) and Purdie 2181 (CANB).

2.4.9. *E. lindleyanus* (Domin) C. E. Hubb.

5 to 6 rows of long cells between the costal zones. Long cells 23.4 to 130 micrometres long (average 81.4); 13 to 26 micrometres wide (average 19.6). 1 short cell associated with each hair base. 2 rows of stomata between the costal zones. Stomata 18.2 to 28.6 micrometres long (average 22.8); 15.6 to 28.6 micrometres wide (average 20.2). Prickles associated with the costal zone 28.6 to 72.8 micrometres long (average 47.6); present on the central portion of the costal zone, or absent. Costal zone 13 to 80.6 micrometres wide (average 45.6). Silica cells 10.4 to 20.8 micrometres long (average 16.1); cross-shaped to dumbbell-shaped. Microhairs 39 to 184.6 micrometres long (average 130).

Leaf blade in transverse section with prominent abaxial ribs only. Abaxial ribs irregular in size; main ribs flattened in outline. Mesophyll chlorenchyma distinctively radiate. Maximum cells-distant count of 1. Inner sheath complete in large vascular bundles; conspicuous in small vascular bundles. Outer sheath interrupted adaxially and abaxially; cells of individual sheaths constant in size; outline of individual sheaths angular in small vascular bundles. Colourless cells commonly traversing the mesophyll. Combined adaxial

and abaxial girders I-shaped. Strands 1 to 4 cells high (common on both adaxial and abaxial ends).

Voucher specimens for anatomical study: Adams 1382 (CANB) and Simon & Andrews 2568 (CANB).

2.4.10. *E. pubescens* (Domin) N. Burb.

5 to 6 rows of long cells between the costal zones. Long cells 15.6 to 117 micrometres long (average 58.6); 10.4 to 26 micrometres wide (average 16.4). 1 short cell associated with each hair base. 2 rows of stomata between the costal zones. Stomata 19.5 to 31.2 micrometres long (average 25.5); 15.6 to 23.4 micrometres wide (average 22). Prickles associated with the costal zone 33.8 to 117 micrometres long (average 89); absent from the central portion of the costal zone. Costal zone 39 to 117 micrometres wide (average 70.8). Silica cells 9.1 to 23.4 micrometres long (average 15); dumbbell-shaped to nodular (rarely cross-shaped). Microhairs 31.2 to 221.1 micrometres long (average 126).

Leaf blade in transverse section nodular (adaxial ribs more prominent). Adaxial ribs irregular in size (large ribs slightly raised above the general level of the small ribs). Abaxial ribs irregular in size; all rounded in outline. Mesophyll chlorenchyma distinctively radiate. Maximum cells-distant count of 1 (rarely 2). Inner sheath complete in large vascular bundles; conspicuous in small vascular bundles. Outer sheath interrupted adaxially and abaxially; cells of individual sheaths constant in size; outline of individual sheaths angular in small vascular bundles. Colourless cells rarely traversing

the mesophyll. Combined adaxial and abaxial girders T-shaped. Strands 2 to 6 cells high (common on both adaxial and abaxial ends).

Voucher specimen for anatomical study: Hubbard & Winders 6763 (CANB).

2.4.11. *E. asperatus* C. E. Hubb.

5 to 6 rows of long cells between the costal zones. Long cells 20.8 to 117 micrometres long (average 66.6); 10.4 to 22.1 micrometres wide (average 15.3). 1 short cell associated with each hair base. 2 to 3 rows of stomata between the costal zones. Stomata 18.2 to 27.3 micrometres long (average 22.2); 13 to 20.8 micrometres wide (average 17). Prickles associated with the costal zone 33.8 to 109.3 micrometres long (average 74.2); present on the central portion of the costal zone. Costal zone 39 to 79.3 micrometres wide (average 55.5). Silica cells 7.8 to 27.3 micrometres long (average 18.1); cross-shaped. Microhairs 28.6 to 171.6 micrometres long (average 84.2).

Leaf blade in transverse section with prominent abaxial ribs only (adaxial surface practically flat). Abaxial ribs irregular in size; main ribs flattened in outline. Mesophyll chlorenchyma not distinctively radiate. Maximum cells-distant count of 1 (rarely 2). Inner sheath complete in large vascular bundles; conspicuous in small vascular bundles. Outer sheath interrupted adaxially and abaxially; cells of individual sheaths constant in size; outline of individual sheaths circular in small vascular bundles. Colourless cells commonly traversing the mesophyll. Combined adaxial and abaxial girders T-shaped. Strands 1 to 4 cells high.

Voucher specimens for anatomical study: Everist 3205 (CANB) and Lazarides 4413 (CANB).

2.4.12. *E. nigricans* (R. Br.) P. Beauv.

5 to 7 rows of long cells between the costal zones. Long cells 18.2 to 182 micrometres long (average 82.2); 11.7 to 23.4 micrometres wide (average 18.2). 1 short cell associated with each hair base. 2 rows of stomata between the costal zones. Stomata 20.8 to 29.9 micrometres long (average 18.7); 18.2 to 31.2 micrometres wide (average 22.2). Prickles associated with the costal zone 28.6 to 72.8 micrometres long (average 50.9); absent from the central portion of the costal zone. Costal zone 13 to 118.3 micrometres wide (average 42.7). Silica cells 10.4 to 27.3 micrometres long (average 18.9); cross-shaped to dumbbell-shaped, or nodular (rare). Microhairs 28.6 to 182 micrometres long (average 76.7).

Leaf blade in transverse section with prominent adaxial ribs only (abaxial ribs barely raised). Adaxial ribs irregular in size. Abaxial main ribs flattened in outline. Mesophyll chlorenchyma distinctively radiate. Maximum cells-distant count of 1 (rarely 2). Inner sheath complete in large vascular bundles; conspicuous in small vascular bundles. Outer sheath interrupted abaxially; cells of individual sheaths constant in size; outline of individual sheaths angular in small vascular bundles (markedly so and with a tendency to have slightly larger cells at corner ends). Colourless cells commonly traversing the mesophyll. Combined adaxial and abaxial girders I-shaped. Strands 2 to 5 cells high (present on adaxial and or abaxial

ends).

Voucher specimens for anatomical study: Campbell 61 (CANB), D & I.
Parer s.n CANB 321759 (CANB) and Hubbard 5643 (CANB).

2.4.13. *E. robustissimus* (Domin) N. Burb.

5 to 6 rows of long cells between the costal zones. Long cells 13 to 106.6 micrometres long (average 54.6); 13 to 20.8 micrometres wide (average 17). 1 short cell associated with each hair base. 2 to 3 rows of stomata between the costal zones. Stomata 20.8 to 28.6 micrometres long (average 23.4); 15.6 to 23.4 micrometres wide (average 19.2). Prickles associated with the costal zone 13.6 to 107.9 micrometres long (average 76.6); present on the central portion of the costal zone. Costal zone 26 to 105.3 micrometres wide (average 61). Silica cells 7.8 to 24.7 micrometres long (average 18); cross-shaped to dumbbell-shaped, or nodular (rare). Microhairs 31.2 to 153.4 micrometres long (average 89).

Leaf blade in transverse section nodular. Adaxial ribs irregular in size (the main ribs slightly raised above the general level of the small ribs). Abaxial ribs irregular in size; main ribs flattened in outline. Mesophyll chlorenchyma distinctively radiate. Maximum cells-distant count of 1. Inner sheath incomplete in large vascular bundles (not clearly defined abaxially); conspicuous in small vascular bundles. Outer sheath interrupted adaxially and abaxially; cells of individual sheaths constant in size; outline of individual sheaths angular in small vascular bundles. Colourless cells commonly traversing the mesophyll (prominently so). Combined adaxial and

abaxial girders I-shaped to T-shaped. Strands 1 to 3 cells high (rare adaxially).

Voucher specimens for anatomical study: Latz 1644 (CANB) and Perry 1669 (CANB).

2.4.14. *E. arenicola* (Domin) N. Burb.

4 to 5 rows of long cells between the costal zones. Long cells 18.2 to 118.8 micrometres long (average 42.5); 10.4 to 18.2 micrometres wide (average 15.3). 1 short cell associated with each hair base. 2 rows of stomata between the costal zones. Stomata 16.9 to 23.4 micrometres long (average 20); 13 to 19.5 micrometres wide (average 16.5). Prickles associated with the costal zone 19.5 to 52 micrometres long (average 34); absent from the central portion of the costal zone. Costal zone 23.4 to 78 micrometres wide (average 47.8). Silica cells 7.8 to 20.8 micrometres long (average 14); dumbbell-shaped. Microhairs 36.4 to 150.8 micrometres long (average 98.1).

Leaf blade in transverse section nodular. Adaxial ribs irregular in size. Abaxial ribs irregular in size; main ribs flattened in outline. Mesophyll chlorenchyma distinctively radiate. Maximum cells-distant count of 1 (rarely 2). Inner sheath complete in large vascular bundles; conspicuous in small vascular bundles. Outer sheath interrupted adaxially and abaxially; cells of individual sheaths constant in size; outline of individual sheaths circular in small vascular bundles. Colourless cells commonly traversing the mesophyll. Combined adaxial and abaxial girders I-shaped. Strands 1 to 4 cells

high (present on both adaxial and abaxial ends).

Voucher specimens for anatomical study: Hubbard & Winders 6435 (CANB), Blake 8206 (CANB) and Tryon s.n BRI 319961 (BRI).

2.4.15. *E. caerulescens* (Gaudich.) N. Burb.

5 to 6 rows of long cells between the costal zones. Long cells 28.6 to 213.2 micrometres long (average 110.3); 10.4 to 23.4 micrometres wide (average 16.1). 1 short cell associated with each hair base. 1 to 2 rows of stomata between the costal zones. Stomata 20.8 to 28.6 micrometres long (average 24.8); 15.6 to 23.4 micrometres wide (average 18). Prickles associated with the costal zone 26 to 84 micrometres long (average 58.2); absent from the central portion of the costal zone. Costal zone 18.2 to 93 micrometres wide (average 33.2). Silica cells 11 to 29.9 micrometres long (average 22.2); cross-shaped to dumbbell-shaped, or nodular (rare). Microhairs 72.8 to 179.4 micrometres long (average 118).

Leaf blade in transverse section with prominent adaxial ribs only. Adaxial ribs irregular in size. Abaxial ribs irregular in size; main ribs flattened in outline. Mesophyll chlorenchyma distinctively radiate. Maximum cells-distant count of 1 (rarely 2). Inner sheath incomplete in large vascular bundles; conspicuous in small vascular bundles. Outer sheath interrupted adaxially and abaxially; cells of individual sheaths constant in size; outline of individual sheaths angular in small vascular bundles. Colourless cells commonly traversing the mesophyll (markedly so). Combined adaxial and abaxial girders T-shaped. Strands 1 to 6 cells high (present on adaxial and

abaxial ends.)

Voucher specimens for anatomical study: Meadley 86 (PERTH) and Craven 5106 (CANB).

2.4.16. *E. cylindricus* N. Burb.

5 to 7 rows of long cells between the costal zones. Long cells 11.7 to 137.8 micrometres long (average 73.4); 11.7 to 23.4 micrometres wide (average 17). 1 short cell associated with each hair base. 2 to 3 rows of stomata between the costal zones. Stomata 18.2 to 128.6 micrometres long (average 77.5); 15 to 23.5 micrometres wide (average 19). Prickles associated with the costal zone 20.8 to 91 micrometres long (average 52); absent from the central portion of the costal zone. Costal zone 23.4 to 54.6 micrometres wide (average 34.2). Silica cells 9.1 to 26 micrometres long (average 13.5); cross-shaped to dumbbell-shaped, or nodular (rare). Microhairs 33.8 to 148.2 micrometres long (average 83.5).

Leaf blade in transverse section nodular. Adaxial ribs irregular in size. Abaxial ribs irregular in size; main ribs flattened in outline. Mesophyll chlorenchyma distinctively radiate. Maximum cells-distant count of 1 to 2. Inner sheath complete in large vascular bundles; conspicuous in small vascular bundles. Outer sheath interrupted abaxially; cells of individual sheaths constant in size; outline of individual sheaths circular in small vascular bundles. Colourless cells commonly traversing the mesophyll. Combined adaxial and abaxial girders I-shaped. Strands 2 to 5 cells high (common on both adaxial and abaxial ends).

Voucher specimens for anatomical study: Parker 232 (CANB) and Nelson 1874 (CANB).

2.4.17. *E. polyphyllus* (Domin) N. Burb.

5 to 7 rows of long cells between the costal zones. Long cells 80.8 to 111.6 micrometres long (average 66.7); 11.7 to 26 micrometres wide (average 17.6). 1 short cell associated with each hair base. 2 rows of stomata between the costal zones. Stomata 18.2 to 29.9 micrometres long (average 23.4); 13 to 24 micrometres wide (average 17.2). Prickles associated with the costal zone 28.6 to 98.5 micrometres long (average 66.2); absent from the central portion of the costal zone. Costal zone 20.8 to 83.2 micrometres wide (average 37.7). Silica cells 10.4 to 28.6 micrometres long (average 18.9); cross-shaped to dumbbell-shaped, or nodular (rare). Microhairs 65 to 226.2 micrometres long (average 126.7).

Leaf blade in transverse section nodular (abaxial ribs more prominent). Adaxial ribs irregular in size. Abaxial ribs irregular in size; main ribs flattened in outline. Mesophyll chlorenchyma distinctively radiate. Maximum cells-distant count of 1 (rarely 2). Inner sheath complete in large vascular bundles; conspicuous in small vascular bundles. Outer sheath interrupted adaxially and abaxially; cells of individual sheaths constant in size; outline of individual sheaths angular in small vascular bundles. Colourless cells commonly traversing the mesophyll. Combined adaxial and abaxial girders T-shaped. Strands 2 to 4 cells high (present on adaxial end).

Voucher specimens for anatomical study: Gauba ANU 3725 (GAUBA) and

Chippendale 1622 (AD).

2.4.18. *E. intermedius* N. Burb.

5 to 7 rows of long cells between the costal zones. Long cells 39 to 153.4 micrometres long (average 90.3); 16.9 to 24.7 micrometres wide (average 20.4). 1 short cell associated with each hair base. 2 to 4 rows of stomata between the costal zones (commonly 2). Stomata 24.7 to 36.6 micrometres long (average 29.2); 19.5 to 31.2 micrometres wide (average 24.7). Prickles associated with the costal zone 33.8 to 98.8 micrometres long (average 60.3); present on the central portion of the costal zone. Costal zone 18.9 to 32.6 micrometres wide (average 54.1). Silica cells 18.2 to 31.2 micrometres long (average 25.1); cross-shaped to dumbbell-shaped. Microhairs 70.2 to 158.6 micrometres long (average 120.8).

Leaf blade in transverse section with prominent abaxial ribs only (adaxial surface flat). Abaxial ribs irregular in size; main ribs flattened in outline. Mesophyll chlorenchyma distinctively radiate. Maximum cells-distant count of 1 to 2. Inner sheath complete in large vascular bundles; conspicuous in small vascular bundles. Outer sheath interrupted adaxially and abaxially; cells of individual sheaths constant in size; outline of individual sheaths angular in small vascular bundles (markedly so). Colourless cells commonly traversing the mesophyll. Combined adaxial and abaxial girders I-shaped. Strands 2 to 5 cells high (present on both adaxial and abaxial ends).

Voucher specimens for anatomical study: Hubbard 7881 (BRI) and Turvey s.n AD 97628089 (AD).

2.4.19. *E. truncatus* Kakudidi

5 to 7 rows of long cells between the costal zones. Long cells 20.8 to 161.2 micrometres long (average 86.5); 10.4 to 23.4 micrometres wide (average 15.9). 1 short cell associated with each hair base. 2 rows of stomata between the costal zones. Stomata 13 to 28.6 micrometres long (average 22); 14.3 to 26 micrometres wide (average 19.8). Prickles associated with the costal zone 20.8 to 75.4 micrometres long (average 46.4); present on the central portion of the costal zone. Costal zone 28.6 to 85.6 micrometres wide (average 47.5). Silica cells 13 to 31.2 micrometres long (average 22); cross-shaped to dumbbell-shaped. Microhairs 42.2 to 202.8 micrometres long (average 115.4).

Leaf blade in transverse section nodular (abaxial ribs slightly prominent). Adaxial ribs irregular in size. Abaxial ribs irregular in size; main ribs flattened in outline. Mesophyll chlorenchyma distinctively radiate. Maximum cells-distant count of 1 (rarely 2). Inner sheath complete in large vascular bundles; conspicuous in small vascular bundles. Outer sheath complete in large vascular bundles; cells of individual sheaths constant in size; outline of individual sheaths angular in small vascular bundles (markedly so with a tendency to have slightly larger cells at the corners, the *Sporobolus* type). Colourless cells commonly traversing the mesophyll. Combined adaxial and abaxial girders I-shaped. Strands 2 to 5 cells high (present on adaxial or abaxial or both ends).

Voucher specimens for anatomical study: Speck 1833 (CANB), Story & Yapp 189 (CANB), and Hubbard 7930 (CANB).

2.4.20. *E. conicus* Kakudidi

4 to 5 rows of long cells between the costal zones. Long cells 28.6 to 124.8 micrometres long (average 70.9); 15.6 to 22.1 micrometres wide (average 18.5). 1 short cell associated with each hair base. 2 rows of stomata between the costal zones. Stomata 14.3 to 28.6 micrometres long (average 22.7); 18.2 to 31.3 micrometres wide (average 22). Prickles associated with the costal zone 33.8 to 78 micrometres long (average 58.2); absent from the central of the costal zone. Costal zone 39 to 144 micrometres wide (average 56.4). Silica cells 15.6 to 31.2 micrometres long (average 22.9); cross-shaped to dumbbell-shaped, or nodular (rare). Microhairs 72.8 to 91 micrometres long (average 81.5).

Leaf blade in transverse section nodular (adaxial ribs more prominent). Adaxial ribs irregular in size. Abaxial ribs irregular in size; main ribs flattened in outline. Mesophyll chlorenchyma distinctively radiate. Maximum cells-distant count of 1. Inner sheath incomplete in large vascular bundles (not clearly defined abaxially); conspicuous in small vascular bundles. Outer sheath interrupted adaxially and abaxially; cells of individual sheaths constant in size; outline of individual sheaths circular in small vascular bundles. Colourless cells commonly traversing the mesophyll. Combined adaxial and abaxial girders I-shaped. Strands 1 to 5 cells high (present on adaxial and or abaxial ends).

Voucher specimens for anatomical study: Latz 948 (CANB) and Nelson 2192 (PERTH).

2.4.20.1. Var. *clelandii* (N. Burb.) Kakudidĩ

5 to 6 rows of long cells between the costal zones. Long cells 41.6 to 142 micrometres long (average 95.4); 13 to 23.5 micrometres wide (average 18.1). 1 short cell associated with each hair base. 2 to 3 rows of stomata between the costal zones. Stomata 20.8 to 29.9 micrometres long (average 25.1); 15.6 to 26 micrometres wide (average 18.5). Prickles associated with the costal zone 36.5 to 88.4 micrometres long (average 64.8); present on the central portion of the costal zone. Costal zone 24.3 to 91 micrometres wide (average 45.5). Silica cells 14.3 to 32.5 micrometres long (average 23.2); dumbbell-shaped. Microhairs 57.2 to 189.8 micrometres long (average 83.2).

Leaf blade in transverse section nodular. Abaxial ribs irregular in size; main ribs flattened in outline. Mesophyll chlorenchyma distinctively radiate. Maximum cells-distant count of 1. Inner sheath complete in large vascular bundles; conspicuous in small vascular bundles. Outer sheath interrupted adaxially and abaxially; cells of individual sheaths constant in size; outline of individual sheaths circular in small vascular bundles. Colourless cells commonly traversing the mesophyll. Combined adaxial and abaxial girders T-shaped. Strands 1 to 5 cells high (present on adaxial or abaxial or both ends).

Voucher specimens for anatomical study: Cleland s.n. AD 96244014 (AD) and AD 97215047 (AD).

2.5. DISCUSSION

2.5.1. ABAXIAL EPIDERMIS

Although the sub-families and tribes of Poaceae are generally distinguished by the morphological characters of the spikelet and inflorescence, it has been known for many years that additional characters may contribute to a more natural and phylogenetic arrangement of taxa. The epidermis has been used extensively in taxonomy (e.g. Prat 1932, 1936; Davies 1956; Tateoka 1957; Metcalfe 1960).

The pattern that emerges from the present leaf epidermal studies has a number of implications. The similar epidermal features exhibited in these species are an indication that they are a natural group. The epidermis is generally a panicoid type with silica cells mostly dumbbell-shaped, cross-shaped or nodular. The presence of bicellular microhairs with sunken bases, and stomata commonly with triangular to tall, dome-shaped subsidiary cells occurring on the same leaf, are all characteristic of the panicoids (Prat 1936; Gould 1968; Metcalfe 1960).

The costal zone is characterized by a mixture of panicoid and festucoid features. It consists of single or paired short cells commonly alternating with silica cells which is a festucoid pattern, but the shape of the silica cells is a panicoid feature.

It is commonly believed by some taxonomists that the festucoids are a less specialized group, but Stebbins (1956) holds the opposite view. Stebbins considers them to be a group which has become

specialized largely by reduction of the leaf epidermis, the embryo, the caryopsis, and the seedling, during their course of evolution. On the other hand the panicoids, though seemingly with a complex epidermis, are considered to have retained less specialized, or primitive, features in the leaf epidermis, the embryo, etc. If Stebbins' view is held, the epidermis of *Enneapogon*, which possesses many panicoid features other than the cell arrangement of the costal zone, is less specialized. This view is supported by Gould (1968), who also asserts that the presence of bicellular microhairs in the epidermis appears relatively primitive and the absence of hairs in the festucoid grasses is more advanced.

However, Brown (1958) pointed out that while grasses have characteristically become specialized by reduction, reduction does not lead to simplicity; rather it leads to complexity - implying that the the panicoids, with a seemingly complex epidermis, are more specialized. According to Brown, the festucoids are near the primitive group and therefore less specialized. If this view is held, it would appear that the epidermis of *Enneapogon* is more specialized. The presence of a festucoid pattern over the costal zone suggests that the process of specialization did not occur at the same rate. Prat (1951) classified this kind of epidermis as intermediate, or the exodermic type, which is characterized by protuberant cells, for example, hairs, spicules, prickles, etc, alternating with long cells. Whatever the relationship of the panicoids and the festucoids to each other (e.g. Stebbins 1956; Brown 1958), the epidermal features of *Enneapogon* show the genus and its close allies to have their affinities among the panicoids.

The stalked-glandular microhairs are unique to the tribe

Pappophoreae, to which *Enneapogon* belongs (Lohaus 1905; Prat 1936; Chippindall 1955; Tateoka et al. 1959; Metcalfe 1960; Jacques-Felix 1962). The bicellular hairs have hemispherical short cells associated with their hair bases. The illustration by Jacques-Felix (1962) shows two hemispherical cells associated with one hair base; a feature not revealed by this study. However, in *E. pubescens* the hemispherical cells are often close to each other, and each is associated with a hair base. If one hair falls off, as is often the case, then it can be mistakenly interpreted as the hair having two or more hemispherical short cells associated with the base.

2.5.2. TRANSVERSE SECTION OF LEAF BLADE

The internal leaf anatomy, as revealed by transverse section, has been emphasized as a fundamental character by many authors. The features exhibited by *Enneapogon* in transverse section show that the species are a natural group; and that any differences may be attributed to habitat conditions or accepted as variability inherent in the species.

The internal leaf anatomy of *Enneapogon* is rather complex in that it exhibits a mixture of characters of major sub-families. These characters are considered here in the light of the opinions expressed by Stebbins (1956) and Brown (1958). Brown expressed the opinion that grasses should be divided into 6 major groups according to leaf anatomy. He considered a number of characters of phylogenetic importance:

"(a) presence or absence of the inner sheath (endodermis

sheath)

(b) structure and function of the outer sheath (parenchyma sheath)

(c) arrangement of the chlorenchyma cells between the bundles

(d) certain physiological aspects associated with (b) and (c)".

According to Brown, the festucoid type is little changed from the original hypothetical type, which consisted of an endodermal sheath of thick-walled cells surrounding the vascular tissue. He asserts that there would have been a distinct parenchyma sheath and the arrangement of chlorenchyma cells would have been irregular, with numerous large intercellular spaces, a rather typical unspecialized spongy mesophyll.

Table 2-1.

Summary of the relationships of Enneapogon and major sub-families.

Abbreviations: I S, inner sheath; O S, outer sheath;
C, Chloridoid; E, Eragrostoid; F, Festucoid;
P, Panicoid.

Enneapogon characters	Major sub-families
Numerous and crowded vascular bundles	P
Double bundle sheath	E - F
Double bundle sheath in main veins	P
Well developed I S with thick walled cells	F
I S complete or interrupted on one side	E - F - P
O S more or less constant in size	E - P
O S cells dark green	E - P
O S complete around small vascular bundles	P
O S interrupted on one or both ends	E - P
Mesophyll of radiate chlorenchyma	C - E - P
Maximum cells-distant count of less than 4	C - E - P
Reduced air space in the mesophyll	C - E - P
Bulliform cells in simple fan groups	C
Colourless cells traversing the mesophyll	C - E
or not traversing the mesophyll	P

From the above table it can be inferred that the Australian Enneapogon species exhibit a specialized internal leaf anatomy

atypical of Brown's (1958) hypothetical type. It is also apparent that the group's affinities are not with the Festucoideae, but rather with the Panicoideae and Eragrostoideae as Prat (1935) suggested. The general outline of the outer sheath in small vascular bundles, a *Sporobolus* character, provides a further clue that the taxonomic affinities of *Enneapogon* are not among the Festucoideae.

Other than the attributes in transverse sections that are useful indicators to the identification of members of *Enneapogon*, a number of points emerge which have various implications. A large amount of supporting tissue in the Australian plants is essential because of the harsh environment to which the plants are exposed. The sclerenchyma accompanying all the vascular bundles offer considerable support to the leaf blades. In some species like *E. pallidus*, almost one-third of the abaxial end of the vascular bundles is accompanied by sclerenchyma 10 or more cells high.

As was observed, the transition of cell size in the inner sheath, that is, cells becoming smaller in diameter and increasingly thick-walled and fibre-like abaxially, seems to be an adaptive feature providing more supporting tissue for the particular conditions to which the plants are exposed.

The outer sheath consisting of translucent to green pigmented large and round cells with relatively thin unlignified walls, has been reported to be almost always present in grasses. However, it is believed that the dark green cells of the parenchyma, typical of the panicoids, andropogonoids, chloridoids and other related groups, are associated with the C4 photosynthetic pathway and for a long period they were used as a C4 indicator. Clifford and Watson (1977) expressed the opinion that the chlorenchyma cells, which are rather

precisely orientated so as to radiate from the vascular bundles, are a better indicator. In addition they consider the 'lateral cells count' to be a more precise indicator of the C₄ photosynthetic pathway than 'radiateness', as the former is easily recordable even from herbarium material, as was used in this study. Brown and Smith (1972) expressed the opinion that detection of any of the aspects of the C₄ photosynthetic pathway denotes its presence. Therefore it can be inferred from observations made in this study that the Enneapogon species with a mesophyll of radiate chlorenchyma and a maximum cells-distant count of less than 4 are C₄ plants.

3. CYTOLOGY: CHROMOSOME COUNTS

3.1. INTRODUCTION

Published cytological information about the tribe Pappophoreae, subtribe Cottineae, to which *Enneapogon* belongs, suggests the basic chromosome number of $x = 10$. Chromosome numbers have been reported for one Indian, four African, and one American *Enneapogon* species. A diploid number of $2n = 20$ has been determined for *E. desvauxii* (Covas 1945; Gould 1960, 1966; Reeder 1967), and $2n = 40$ for *E. cenchroides* (Reeder & Singh 1968). However, de Wet & Anderson (1956) and de Wet (1958) reported a chromosome number of $2n = 36$ for *E. brachystachyus*, *E. cenchroides*, and *E. scoparius*, and $2n = 18$ for *E. pretoriensis*; numbers which would mean a basic chromosome number of $x = 9$, as well as $x = 10$. De Wet (1954) suggested $x = 12$, which would mean that species with $2n = 36$ are triploids. Reeder and Singh (1968) subjected those species, for which the chromosome numbers of $2n = 36$ and $2n = 18$ were reported, to further cytological studies in view of the fact that there appeared to be more than one basic chromosome numbers not only in the subtribe Cottineae, but also in one genus. From their studies they consider that the basic chromosome number of this genus is $x = 10$.

Australian *Enneapogon* species are poorly known cytologically. Thus an effort was made to determine chromosome numbers for some species and the results are tabulated below.

3.2. MATERIALS AND METHODS

Seeds secured from herbarium specimens were germinated on filter paper to provide roots free from dirt. These were cut as soon as they were 1 to 2 cm long and pretreated with 0-isopropyl-N-phenylcarbamate (IPC) for 2 to 3 hours to arrest cell division and cause contraction of the chromosomes. The roots were then fixed in Farmers fluid (3 parts of absolute alcohol to 1 of glacial acetic acid solution) for a period of 12 to 24 hours. The fixative was washed out in 3 changes of alcohol (70%) for 1 hour each and stored in the last change at temperatures below -6 C until required. Before squashing, the roots were warmed in 1N HCl on a water bath at 60 C to effect hydrolysis and dissolve the pectic substances of the middle lamellae to separate the cells and then stained in aceto carmine.

3.3. RESULTS

Table 3-1 lists the chromosome numbers obtained; the collection numbers of the specimens studied are also listed; the numbers in brackets against the species indicate the number of collections examined. Probably due to age of the collections and treatment in the herbarium, few specimens tested yielded viable seeds. With regard to the counts, the species are diploids and indicate a conformity to the tribal pattern of $x = 10$. Unfortunately the counts can only be regarded as tentative as, due to their small size, the chromosomes from the root tips were found difficult to count.

Table 3-1.
Chromosome numbers.

Species		Count	Collector/No.	
E. avenaceus	(2)	20	Latz	1685
"		20	Shearer	126
E. caerulescens	(1)	20	Weber	2821
E. cylindricus	(1)	20	Kuchel	2929
E. conicus	(1)	20	Nelson	2129
E. decipiens	(1)	20	Latz	21365
E. intermedius	(1)	20	Weber	8562
E. oblongus	(1)	20	Williams	3221
E. pallidus	(1)	20	Byrnes and Maconochie	1055
E. eremophilus	(1)	20	Latz	21107
E. polyphyllus	(1)	20	Molenmans	654
E. robustissimus	(1)	20	Latz	1644

3.4. DISCUSSION

Enneapogon species are a markedly uniform group in many respects. Because of the similarity existing between the species and the intergradation in some cases of even the most constant characters, the taxonomy of this group of species is difficult. It was hoped that the cytological study might aid in the clear understanding of the taxonomy of the Australian Enneapogon species. However, it appears

that the anatomical and morphological uniformity extends to cytology.

The present report of chromosome determinations represents about 50% of the Australian *Enneapogon* species. Such a homogeneous group, cytologically, is very unusual in Poaceae and contrasts sharply with the more typical, polyploid, condition as found in most genera of higher plants (Love 1964; de Wet 1971), and in some particular Australian species, e.g. *Themeda australis* (Hayman 1960). Polyploidy seems to be operative in speciation of most grass genera, with aneuploidy being supplementary in others. The interpretation of the situation in the Australian members of *Enneapogon* is therefore difficult.

In the Australian *Enneapogon* species, there is no evidence of change in the chromosome numbers. As very few representatives of the particular species were examined cytologically, the survey is not exhaustive, but the constant chromosome numbers are an indication that the species form a natural group. With few exceptions, contemporary evolutionists agree that geographic speciation is the predominant mode in diploid outbreeding organisms (e.g. Mayr 1963, 1970, 1976; Dobzhansky 1970; Grant 1971, 1977). According to these authors, the mode involves a division of a continuous population into 2 or more geographical isolates, which diverge in response to local pressures and develop fixed isolating mechanisms which would prevent gene exchange if isolates become sympatric. It is apparent that differences in adaptability within the group operate throughout the region, as revealed by the distribution of different species (Maps 1-13b). It is rather difficult to relate this difference to any one factor as many factors may have interacted to produce the current state of affairs. However, climate, and to some extent soil, is considered to be a major

operative factor in Australian species distribution, which in turn results in the restriction of gene pools.

Compared with the past climatic periods that started in the middle Miocene, in which there were cycles of cooling and warming leading towards aridity and which became increasingly marked by seasonality in precipitation (Barlow 1981), the climate would still be more or less similar to today. Therefore, the species evolved in similar conditions and thus the diploids have possibly been in Australian Enneapogon for a long time. Darlington (1956) pointed out that where chromosomes are less stable they reflect what is happening at this time to the races and species; and where the chromosomes are more stable they represent what happened in the former geological and evolutionary epochs. The Australian Enneapogon species appear to belong to the latter, that is, they provide a record of the past, a living record, significant in a surprisingly similar way to the dead record which the fossils provide.

The Australian members of Enneapogon belong to the Gondwanan element (Clifford & Simon 1981), and various studies have strengthened the argument favouring the presence of an ancient Gondwanan element in the Australian flora (e.g. Burbidge 1960; Barlow 1981; Johnson & Briggs 1975, 1981; etc). These authors have discussed the subject at length and a number of points that emerge can be related to Enneapogon.

It is apparent that in Enneapogon the pressure, if any, has been directed at maintaining the status quo, that is, the diploid chromosome numbers. However, the morphological variations are probably a result of different isolating mechanisms. Barlow (1981) pointed out that the increased separation of Australia from other major

continents, followed by climatic changes involving temperatures, precipitation and seasonality, etc, favoured an increase in habitat differentiation. Like the other Gondwanan flora which underwent differentiation under conditions of varying habitats, it appears that Enneapogon underwent differentiation which gave rise to the present or near-present species. Mayr (1963) pointed out that to be a different species is not a matter of difference, but one of distinctiveness. Therefore, the result was the external differences of form, by which they are recognised by the taxonomist without necessarily any changes in the chromosome numbers. Thus the present Enneapogon species can be regarded as a derived element. Barlow (1981) indicated that such derived elements are a result of a considerable evolutionary change under conditions of geographical isolation which led to habitat differentiation, and thus ecological isolation, to produce the typical taxa with high endemism. This isolation probably affected chromosome numbers through a cleavage of the breeding groups of Enneapogon, which is apparent from the present day distribution and discontinuity of the phenotypes.

It is likely, of course, that there are infraspecific differences in genomes, but this has not been proved in the present study. Even if allowance is made for infraspecific differences the resulting pattern has been one of adaptation and evolution to a harsh, mostly arid, environment which produced a differentiation of the adaptive biotype but conserved the chromosome numbers. The occurrence of Enneapogon species in both arid and non-arid zones is an indication that numerous independent and parallel lines of adaptation and conservation have occurred throughout the region.

4. AXILLARY CLEISTOGAMY

4.1. INTRODUCTION

Cleistogamy has been reported in numerous grass genera and species, many of which are highly specialized in this type of reproduction. Connor (1979) estimated its presence in 70 genera.

Harlan (1945) pointed out that the first description of cleistogamy in a species was made by William Jackson Hooker in 1840, when he described and named the species *Ceratochloa grandiflora*, and later reduced it to a synonym of *Bromus carinatus*.

Cleistogamy occurs in 4 different forms according to Harlan (1945). Of these forms that cleistogamy may take, subterranean cleistogamy is considered to be the most unusual. The spikelets are borne underground on short stalks. The hidden spikelets or cleistogenes were first fully described by Chase (1908, 1918). She noted that these cleistogenes were so different morphologically that the plants would be placed in a different tribe were chasmogamous flowers not available. Chase (1946) defined cleistogenes as solitary, single florets without glumes, which are borne in the lower sheaths, and clasped by wings of an indurated prophyllum. In this study cleistogenes are defined as single or more spikelets that are borne in the sheath axils, and clasped by broadened, almost bladeless sheaths when borne at the lower nodes.

In the tribe Pappophoreae, to which *Enneapogon* belongs, cleistogamy has been reported in *Cottea*, *Pappophorum*, and *Enneapogon*. In the Australian members of *Enneapogon*, axillary cleistogenes have

been observed in 3 species. The first one, *E. asperatus*, was reported by Hubbard (1937). Later Burbidge (1941) added *E. caerulescens* and *E. cylindricus*. These species have been re-examined. A kind of cleistogamy was also observed in *E. polyphyllus*.

4.1.1. *E. asperatus*

In *E. asperatus* the axillary cleistogenes are enclosed in the uppermost leaf sheaths. The spikelets in the sheaths are practically unmodified, that is, they are characteristic of the species. They differ from those in the terminal panicle only by a slight increase in size and the glumes are membranous rather than coriaceous. Burbidge (1941) commented that such axillary cleistogenes are released by the disarticulation of the culms at the upper nodes. However, such a phenomenon was not observed in the material examined during this study, but the possibility cannot be ruled out.

4.1.2. *E. cylindricus*

In this species disarticulation at the nodes is common. The axillary cleistogenes occur in axils of sheaths along the culms and are sometimes semi-exserted. The exserted spikelets behave chasmogamously. The cleistogamous spikelets are practically unmodified, but have membranous glumes. The caryopses in these florets are dispersed when the culms break up at maturity.

An interesting feature in this species is the development of somewhat modified cleistogenes in the axils of broadened more or less bladeless sheaths. About 1 to 3 spikelets develop within the axils of these sheaths. They are 5 to 6 mm long (the terminal ones often longer than the lateral ones), lanceolate, 4 to 5-flowered, with 1 fertile floret per spikelet, and somewhat gibbous. The glumes are 6 to 7 mm long (in contrast to 2 to 5.6 mm long in terminal panicle spikelets), elliptic to lanceolate, membranous. The lower glume is pilose, the upper glume glabrous. In nervation they fall within the range exhibited in the spikelets of the terminal panicles, that is, 4 to 8 nerves. The body of the lower lemma is 2.5 to 3.5 mm long (average 2.9), in contrast to 1.9 to 3.5 mm long (average 2.5) for the lower lemmas of the spikelets of the terminal panicles. The caryopses are also slightly larger, 2 to 2.2 mm long, elliptic.

Dispersal mechanisms for such caryopses are not very clear but as Burbidge (1941) suggested, they are probably dispersed when the sheaths dry and break away. However, on examining the material available to me, it was noted that most of these cleistogenes develop just below the soil surface so that the above means of dispersal would not be possible, except for the caryopses to germinate within their enclosure, thus increasing the size of the tufts. Another interesting feature concerning these cleistogenes is that they are common in specimens from grazed or dry habitats in contrast to those collected from or near well watered habitats like river and stream banks, etc.

4.1.3. *E. caerulea*

The species differs from *E. cylindricus* by not having disarticulating culms. The axillary cleistogenes consist of 1 to 3 spikelets, rarely more, and the whole structure is enclosed in a basal sheath with reduced lamina. As reported by Burbidge (1941) and also observed in this study, the terminal spikelets mature first, while the lateral spikelets may or may not mature. The lateral spikelets are often with undehiscent anthers or sometimes abortive.

The spikelets are not modified but are slightly larger and have membranous glumes, in contrast to the coriaceous ones of the terminal panicles. Spikelets 5.5 to 7 mm long (average 6.9), lanceolate; the lower glume 4.6 to 6. long (average 5.3), lanceolate; the upper glume 4.9 to 6.8 mm long (average 5.9), elliptic; awns 2 to 6 mm long (average 3.9); the body of the lowest lemma 2.3 to 3 mm long, 2.2 to 2.6 mm wide (average 2.4). The hairs on the lemma are shorter than, or as long as, the body in contrast to those of the lemmas of the spikelets from the terminal panicles which are longer.

As in *E. cylindricus*, axillary cleistogenes were not found in specimens with an annual habit and those collected from well watered habitats. No axillary cleistogenes were found in *E. caerulea* var. *occidentalis* which has an annual habit.

4.1.4. *E. polyphyllus*

In this species the terminal panicles are sometimes semi-exserted. The spikelets remaining in the sheath of the uppermost

leaf behave cleistogamously, but are not modified in any way. Other species in which axillary inflorescences rarely occur are *E. erimophilus* and *E. oblongus*; the spikelets are typical of the species.

4.2. DISCUSSION

4.2.1. SIGNIFICANCE OF CLEISTOGAMY

E. asperatus, *E. cylindricus*, and *E. caerulescens* occur in areas with erratic rainfall and sparse vegetation. The presence of cleistogenes is thus probably a suitable breeding system for the most extreme environments, though this is difficult to prove in reality and therefore can only be interpreted with caution. The species are facultatively cleistogamous and therefore self-fertility is a reliable system ensuring the production of seed despite an unpredictable environment. Flowering, for example, the opening of flowers, and fruiting are energy and water consuming functions. Therefore, because of the restrictions imposed by the environment, it is more economical to reproduce cleistogamously.

Other species that occur with the above 3 species do not produce axillary cleistogenes of the type that are found in these. While axillary cleistogamy may be an acquired mode of reproduction for survival and continuity of the life cycle, self-fertility is generally common in the species that occur in the dry habitats with the three. In the material examined, unopened florets were often observed in the terminal panicles which developed to maturity. In these species the

dehisced anthers often cling to the tip of the grain. A possible explanation for the absence of axillary cleistogenes in annual species would be that they are not produced in the first year of the plant's life cycle. However, environmental control of cleistogamy has been suggested. For example, Harlan (1945) observed in *Bromus carinatus* that the optimum conditions for flowering usually favoured chasmogamy while adverse conditions tended to force the plant into cleistogamy. Brown (1952) showed that in *Stipa leucotricha* cleistogamy could be a response to low soil moisture; and Langer & Wilson (1965) demonstrated in *Bromus unioloides* that photoperiod and soil moisture were important. That is, short days (< 16 hours) promoted chasmogamy when the soil moisture was high, and the inflorescence was wholly or partly chasmogamous in a 10.5-hour day while a 16-hour day promoted cleistogamy. When in a 12-hour day and in dry soils *B. unioloides* was cleistogamous, but in the same day-length and wet soils chasmogamy was promoted. Although not proved in this study the environmental conditions of the Australian interior, possibly coupled with the photoperiod, are the most plausible explanation for the promotion of cleistogamy in the Australian members of *Enneapogon*.

5. MORPHOLOGY: A REVISION OF ENNEAPOGON

5.1. INTRODUCTION

The Australian members of *Enneapogon* were last revised by Burbidge (1941). She recognised 19 species, many of which remained poorly defined and accordingly caused a certain amount of trouble to botanists who deal with the species both in the field and in the herbarium. Many workers encountered these problems as early as the last century. Mueller (1872) considered all the Australian material to belong to one species *Pappophorum commune*. Later Bentham (1878) in compiling the *Flora Australiensis* recognised two species. Being sure only concerning *E. avenaceus*, he regarded the rest of the Australian material as belonging to one species *E. nigricans* but with the following note (Bentham assigned the species to *Pappophorum*):

"Evidently a very common plant and most variable in aspect, and it seems at first most difficult to unite the small slender *P. gracile*, Br., with a looser pale spike and rather narrow spikelets, with the stouter larger typical dark-coloured plant with dense cylindrical spikes, but, on going through the long series of specimens before me in different stages of development, I failed in sorting them into distinct varieties, and felt obliged to follow F. Mueller in regarding them all as one species, with the exception of the following (*P. avenaceum*) about which I feel some doubts."

More recent workers have had similar problems. Jessop (1981) has this to say:

"*E. clelandii* N. T. Burb. Closely similar to *E. pallidus* and possibly conspecific. Plants of *E. clelandii* apparently differ in habit and indumentum, but *E. pallidus* is highly variable and morphological differences between the two taxa appear to be lacking."

After surveying the previous treatments prior to, and that of Burbidge (1941) plus many Australian regional floras, and in the light of remarks such as those of Bentham and Jessop, it is apparent that the specific limits had become vague and ill-defined and that there is a need for circumscription and further description. Examination of recent collections and also some of the old ones has revealed species not previously recorded in Australia, and some names misapplied. Some nomenclatural errors have also become apparent. Thus the aims of this study are:

- a) recognition of diagnostic characters suitable for the accurate description and circumscription of the taxa based on gross morphology
- b) typification of the taxa
- c) solution of nomenclatural problems
- d) definition of the distribution of the taxa.

5.2. MATERIALS AND METHODS

The study was made on dried herbarium material. Specimens

were received from the following herbaria: AD, BRI, CANB, CGE, GAUBA, K, MEL, NSW and PERTH. The herbaria are abbreviated for each institute, as listed in the Index Herbariorum I, 7 ed. (Holmgren et al. 1981). A critical examination was made on representative specimens mostly from CANB plus a few from other herbaria as indicated in the representative specimens. Care was taken to include a full range of geographical, ecological, and morphological variation. The rest of the material was examined and annotated.

A computer was used to generate the key and the descriptions of the species. In his study of *Digitaria*, Webster (1983) first applied the system to the presentation of a plant taxonomic revision at the species level; and outlined the advantages of the system and how it works. A list of characters was coded in the DELTA format (Dallwitz 1980a, b) for each taxon. Coded data were analysed by KEY (Dallwitz 1978) to produce the key to the species using only morphological characters. Character weights, ranging from 0 to 9, precede the key. These weights correspond to the characters in the descriptions. Higher weights of 5 to 9 were given for characters important for recognition of the species. Characters of little or no taxonomic importance were weighted 1 to 4, to be used as secondary or supporting characters. Characters to be excluded from the key were weighted zero. The key given here has been selected from a number of experimental attempts using various weighting of parameters.

5.3. CHARACTER EVALUATION

This section is aimed at the discussion of the characters

used in the descriptions and it is hoped that it will help in the understanding of the descriptions and use of the key.

Synonyms are treated as a comment under character 1. Authors are abbreviated in accordance with the recommendations proposed in the Draft Index of Author Abbreviations, Kew (1980) and the herbaria in accordance with Index Herbariorum I, 7ed. (Holmgren et al. 1981). Literature citations are abbreviated, where possible, according to Stafleu (1967) and Stafleu and Cowan (1976, 1979, 1981 & 1983).

(2) Categorization of the plants as annuals or perennials was based on morphological features alone. Plants with hard, contracted rootstock were coded perennials. For some taxa it is possible to have both habits, as the morphological perennial species act as annuals in dry habitat conditions. (3) The flowering culms are tufted. (4) The length of the culms was recorded from mature culms with fully emerged inflorescences inclusive. The importance of this character to identification is limited as the ranges of culm heights for different taxa overlap, possibly due to differences in habitat conditions. In general terms *Enneapogon robustissimus*, *E. pallidus*, *E. conicus*, and *E. intermedius* are robust species and commonly more than 50 cm high. (5) Most taxa have erect culms, but rarely slightly geniculate and ascending at the first or second node in *E. caerulescens*, *E. polyphyllus*, and *E. nigricans*. (6) Branching in most Australian members of *Enneapogon* takes place randomly along the culm; (7) branching that is concentrated at the upper or lower nodes provides a valuable distinguishing character between taxa. This character, however, may not be clearly defined in some instances as grazing may cause such branching in taxa that are commonly branched randomly along the culms. It was noted from herbarium specimens that in *E.*

lindleyanus, regrowth after a fire or grazing tended to produce a kind of branching that is common in *E. pubescens*. In such doubtful instances the old culm remains, if available, were found to be useful in determining the position of the branches. (8) The breaking up at nodes in mature culms is characteristic of *E. cylindricus*. (9) Pubescence or lack of it was recorded from mid-culm nodes. This character is of little value in distinguishing species and if the specimens are not properly handled the hairs are glabrescent. (10) The internodes are either hairy or glabrous; pubescence is limited in identification of species as there is some degree of variability. (11) The length of the sheaths in relation to their internodes is generally variable and of low taxonomic importance; (12) pubescence of mid-culm sheaths is variable. (13) The ligule length does not show marked discontinuity and thus does not constitute a useful taxonomic character. (14) The length was recorded for the mid-culm leaf blades from the ligule to the tip; and (15) the width of the same blades was recorded for the widest part. In general terms these characters are of little importance as there is considerable overlap between the species. (16) The leaf blades are flat or more or less broadly V-shaped. Allowance must be made for the different habitats; and especially for the drying process in the herbarium. Even the basically V-shaped leaf blades tend to be inrolled on drying during their life cycle, or when collected and not promptly pressed; such leaves were coded as involute; the flat leaves tend to curl when sun-dried. (17) The surface texture of leaf blades provides a valuable taxonomic character; the character was recorded for the abaxial surface. Antrorsely scabrous leaves have the prickles turned towards the tip of the blades; retrorsely scabrous leaves have the prickles turned in the

opposite direction. The vestiture of the leaf blades both (18) adaxially and (19) abaxially is subjected to an inconvenient degree of variability especially in species that occur across ecological zones. (20) The leaf blades taper gradually towards the narrow acuminate apices, but in some species they are extended into brown and hair-like structures. (21) The margins have well developed spicules that are antrorsely or retrorsely serrulate, but a mixture of the two may occur on the same margin.

The inflorescence length is considerably variable and ranges overlap and thus it is of little importance for distinguishing between species; the length also tends to be influenced by external factors. (23) The form of panicles was divided into two states: namely, the densely contacted panicles have their lateral branches concealed by the spikelets; and in the loosely contracted panicles the branches are exposed. (24) The shape of the panicles is variable and it may be interrupted by lateral branches; it is cylindrical in *E. cylindricus* and cone-shaped in *E. conicus*. (25) Other than the terminal inflorescences, axillary inflorescences occur in some species; (26) related to the axillary inflorescences is the presence of cleistogenes in axils of the lower or upper sheaths. (27) The spikelets in situ in a panicle are generally about the same length, but are longer towards the apex in *E. caerulescens* in which the upper florets mature first. (28) The length of the spikelets was taken from below the glumes to the tip of the longest awn. The importance of this character is limited as the ranges overlap for most species, possibly due to their positions on the branches and to external ecological factors. (29) Spikelet shape was divided into two states depending on the location of the widest point: namely, lanceolate with the widest point in the

lower one-third, and ovate with the widest point in the lower one-half. The shapes may not be well defined especially when the mature awns open out. (30) The number of florets per spikelet is variable for many species and therefore of limited taxonomic value; (31) of taxonomic importance is the number of bisexual fertile florets, the male florets are occasional in a few species. (32) Spacing of florets along the rachilla was coded for crowded where the sterile florets above the second floret are pressed closely to each other, and not crowded where the florets are well spaced along the rachilla. (33) Sterile florets above the second floret were coded for reflexed if they were bent backwards more than 45 degrees, or not reflexed if divaricating at an angle between 10 to 45 degrees.

(34) The glume length relative to each other is of little taxonomic importance. (35) For many species the glumes are pilose but glabrous glumes distinguish *E. arenicola* from closely related species. (36) Two states of glume texture were recognised: coriaceous glumes are leathery and thicker than the membranous ones which are rather thin. (37) The importance of glume colour is limited as it often fades with prolonged keeping to straw-coloured; the character was recorded for specimens collected before seeding in which the colour tends to be preserved. (38) Colour of the glume margins was recorded for the part between the peripheral nerve and the margins. They were coded for pale green if whitish or pale green, and purplish if tinged with pink to purplish colour. The character is not reliable as the development of the latter appears to depend on exposure to the sun. (39) Glumes with jagged and gnawed apices were coded erose, and those tapering smoothly to a point were coded not erose; this character is consistent for many species. (40) Glumes were coded as concealed if hidden by overlapping

awns, and not concealed if the upper parts of the glumes can be seen in situ; the character was recorded from the middle part of the panicle. (41) Even with precise measurements using a calibrated dissecting microscope the lower glume length is of little taxonomic importance to distinguish closely related species, and the ranges for many species overlap. (42) The number of nerves on the lower glume was taken for the number traversing the widest part of the structure; the character is variable. (43) The shape of the apex of the lower glume varies from truncate, obtuse, acute acuminate to mucronate for many species, so that the character is of little importance. (44) The lower glume shape was divided into three states: oblong for glumes with sides almost parallel, elliptic for glumes with the widest part at the middle and equally tapered at either end, and lanceolate to ovate for glumes with the widest part below or at the middle and tapered at the upper end. Like the lower glume, their upper glume counterparts: (45) the length; (46) the number of nerves; (47) the shape of the apex; and (48) the shape of the glume; are of little taxonomic importance.

Characters of the lower lemma in *Enneapogon* are highly diagnostic and can be used to identify many taxa. (49) The length of the lower lemma was taken for the part below the awns, i.e., the body; it is variable for many species. (50) The width of the lemma was taken at the widest point with the structure opened. (51) The apex of the body of the lower lemma is formed by the awn bases. (52) The number of nerves on the lower lemma is fairly constant for many species but of little taxonomic importance; (53) extra nerves occur between the main nerves and do not often extend to the awns. (54) One nerve entering a peripheral awn was coded when the main nerve alone extended to the

awn, or two when the adjacent extra nerve also extended to the same awn as the main nerve. Although the Australian members of *Enneapogon* can be divided into two main groups based on surface features of the lemma body, variations occur in the ribbed lemmas. (55) Deeply ribbed lemmas were coded for the body with ridges as deep as the furrows, and shallowly ribbed for ridges slightly raised above the furrows; (56) lemmas ribbed on the upper part were coded for the presence of ridges not reaching the base of the lemma, and not ribbed when the nerves are not raised above the surface but appear as strands within the body. (57) The surface texture of the lemma body, especially when papillose, is a matter of degree and somewhat variable for many species. (58) Colour of the lemma is not a reliable character as it is not always preserved in mature or herbarium specimens, and is also variable for species that occur across ecological zones. (59) The shape of the lemma body was determined only for structures that flattened without tearing. (60) The shape of the back of the lemma was coded for convex if having a curvature that bulges, or straight if lacking the curvature. (61) The vestiture of the lemma body was divided into 3 states: hairy all over, for hairs covering the entire body; hairy on the lower part with the upper one-half to one-third glabrous; and glabrous when only with a tuft of hairs at the base and the body lacking hairs. (62) Hair length relative to the lemma body is constant for many species and was divided into 3 states: longer than the body when the hairs arising at any part of the surface overtopped the apex; or as long as the lemma body when the hairs equalled but did not overtop the apex; and shorter than the body when the hairs were shorter than the apex. (63) The margins were coded ciliate if having a fine row of hairs that are more or less horizontal as opposed to those

on the back of the body, or glabrous if entire and lacking the fine row of hairs; (64) the presence of hyaline lobes forming the margins serve to distinguish *E. avenaceus* from other species. (65) The ratio of width to the length of the lower lemma body can be capitalized on after precise measurements using a calibrated dissecting microscope; (66) the ratio of the length of the body to awn length is of little taxonomic importance and variable for many species. (67) The number of awns often corresponds to the number of nerves on the lemma body, each awn containing a continuation of a nerve. In some cases the number is less than the awns due to the extra nerves that do not continue into awns. (68) The length of awns was taken from the bases of the middle awns to their tips; (69) the relative length of awns was recorded for the middle awn and adjacent awns; the awns were coded subequal if the difference between their length was less than 1.0 mm. (70) A ridge, like the knuckles of a hand occurs at the awn bases in some species. (71) As with colour of the other parts, the colour of awns is often faded in sun-dried specimens or at long keeping. (72) A rim of cilia inside the lemma body at the base of the awns, resembling a ligule on a leaf, occurs in many species; its absence serves to distinguish *E. eremophilus* from closely related species.

(73) The palea is often curved over the caryopsis; the length was taken after slight straightening but taking care not to tear across the margins. (74) The palea was coded hairy between the nerves if partially or fully hairy; (75) for most species the apices of the palea are cleft, that is, they have a sinus with acute or acuminate lobes. (76) The vestiture of the palea apex was divided into two states; it was coded glabrous if the upper one-half to one-third lacked hairs. (77) The flaps of the palea are the portions beyond the

keels that are more or less bent inwards. (78) The rachilla, like most other parts, is hairy; the presence of a tuft of hairs between the lower two florets was coded for hairs that are concentrated at a point and longer than the general pubescence. (79) For many species the nerves on the lemma of the second floret are not distinctly ribbed, but their presence serve to distinguish closely related taxa; (80) hairs occur on the back of the second lemma in some species. The hairs are readily glabrescent in some species and can be removed if the specimens are not carefully handled during examination.

(81) Anther length is of little taxonomic importance as the ranges for many species overlap; (82) the colour of the anthers is not reliable as it is often faded in herbarium or sun-dried specimens. (83) The caryopsis length, and (84) the width were coded for mature caryopses; the characters are of little taxonomic importance as the ranges for many species overlap. (85) The shape of the caryopses was divided into 3 states depending on the location of the widest point: globoid for caryopses that are more or less spherical, obovate for caryopses with the widest part above the middle, and elliptic with the widest part at the middle. The embryo length was recorded for the structure constricted in the middle in surface view, and excluding the cotyledon. (86) The ratio of the embryo length to caryopsis length can be used after precise measurements but it is of little taxonomic importance; (87) the embryo length is variable for many species.

5.4. PRESENTATION OF DATA

Within the descriptions of taxa the measurements of various

organs are cited in the following fashion: "lower glume 2.5 to 6.5 (average 3.9)" and "5 to 11-nerved (frequently 7-8)". Figures outside the brackets indicate the recorded range, and those inside the brackets indicate the calculated average from the mean of 30.

Notes on nomenclatural and typification problems, and affinities, where warranted, are outlined following the description for each taxon. Notes on distribution and ecology were compiled from collector's notes except where indicated.

A list of selected representative specimens is cited for each taxon. In cases where a few specimens were available all are cited. The total number of collections seen by the author for each taxon is indicated in brackets, for example, (25/250) where 25 equals the number of representative specimens used in the description of the particular taxon and 250 equals the total of all the specimens seen for the same taxon. Information available on each has been reduced to locality, collector and number, and herbarium. The herbarium sheet number is only cited when the collector's number is not available and date of collection if the forementioned are not available. A list of important references, other than the literature already cited, which contribute to the knowledge of the taxon in terms of nomenclatural history, distribution, etc, and contain good illustrations for the particular taxon, is given where possible, and concludes the treatment for each taxon. The distribution maps are based on the specimens examined by the author. When the number of specimens became excessive for any locale further plottings were not made there.

5.5. TAXONOMIC HISTORY

The first publication of the genus *Enneapogon* appears to have been that of Beauvois (1812), in which he included 4 species described by Robert Brown (1810) under *Pappophorum* Schreb., and *E. desvauxii* P. Beauv. *E. desvauxii* being the only one illustrated, was chosen as the type (Hitchcock 1951). Later Desvaux in 1813 included notes on the genus and acknowledged the first publication as that of Beauvois. As Burbidge (1941) suggested, probably Beauvois attended a meeting at which Desvaux read a paper and received permission there, or at some later time, to publish the genus in his *Essai Agrostographie* on whose preparation he was involved at the time. Whatever the case the two seem to have been in correspondence which would probably explain the inclusion of *E. desvauxii* in Beauvois' publication, a species believed to have been first described by Desvaux, and the authority given for the genus at the first publication. Until recently various author citations have been employed, (e.g. Gardner 1931, Burbidge 1941, Jacques-Felix 1962, Jessop 1981, etc), which failed to give credit to Beauvois for the first publication of the genus, or to show that Desvaux was responsible for the first diagnosis and notes on *Enneapogon*.

The first Australian material to be described was that of Robert Brown (1810). Four species were described under *Pappophorum* Schreb., namely *P. nigricans*, *P. pallidum*, *P. purpurascens*, and *P. gracile*. Later these were transferred to genus *Enneapogon* Desv. ex P. Beauv. by Beauvois in 1812. They have been since regarded as distinct species although Mueller (1872), having failed to distinguish between the material available to him at the time, proposed a name *P. commune*.

for the whole of the Australian material: a name which is illegitimate.

The next species to be described was *P. caerulescens* by Gaudichaud in 1826 (Burbidge 1941). Another significant step was taken by Lindley following Mitchell's expeditions to northern New South Wales. Lindley (1848) described 3 new species, namely *P. flavescens*, *P. avenaceum*, and *P. virens*. Later Bentham (1878), in compiling his *Flora Australiensis*, recognised only 2 species. He kept *P. avenaceum* Lindl. distinct, but combined the rest of the material under *P. nigricans* R. Br. The latter has been a confused species since Bentham's publication. Domin (1915) revised it as *P. nigricans* var. *Brownianum* Domin. He unfortunately included some material of *P. gracile* (R. Br) *P. Beauv.* in his list. Although *E. nigricans* is still upheld as a distinct species changes in its delimitation have been necessary.

Burbidge (1941) examined *P. virens* Lindl. and reduced it to a synonym of *E. gracilis* (R. Br.) *P. Beauv.* Present examination of Mitchell's type specimen on which Lindley based the description showed that it is a distinct species. It has been described as *E. virens* (Lindl.) Kakudidi. *P. flavescens* Lindl. was considered distinct by Burbidge and separated from *E. nigricans* on the basis of having a strongly ribbed lemma with a straight back and a tendency to form loosely contracted panicles. Present examination of the type of *E. flavescens* (Lindl.) N. Burb. showed that the specimen is *E. nigricans*. It is apparent that Lindley did not see Brown's type specimen of *E. nigricans*. It is also apparent that Burbidge's (1941) description of *E. flavescens* is not based on Mitchell's type specimen used by Lindley which she cited, but on the illustrated specimen, Hubbard 7930. This

specimen is distinct from *E. nigricans* and does not agree with its type. The name *E. flavescens* was misapplied to Mitchell's specimen and therefore becomes a synonym of *E. nigricans*.

Bentham's (1878) arrangement in which only 2 species were recognised was followed until Domin's publication of the results of his Queensland collection in 1910. Following his Queensland expedition Domin visited Kew and examined the material available there. As a result of this visit, Domin (1912) published *P. nigricans* var. *barbinode* which was based on Clement's specimen collected between the Ashburton and De Grey rivers, N. W of Western Australia. Burbidge (1941) recognised it as a distinct species from *E. nigricans* and described it as *E. oblongus* N. Burb. However, present examination of the specimens showed that it represents *E. caerulescens* (Gaudich.) N. Burb. Later Domin (1915) published his full results. He described one new species *P. lindleyanum* which he thought might include *P. flavescens* Lindl. It would appear from the text that Domin did not see Lindley's specimen at Cambridge. Domin described 5 varieties under *P. lindleyanum*, namely *convolutum*, *pubescens*, *glaucum*, *laguroides*, and *scaberrimum*. Variety *convolutum* is the type of *P. lindleyanum* and was revised as *E. lindleyanus* (Domin) C. E. Hubb. Under var. *convolutum*, Domin mentioned a larger specimen from Chillagoe in Queensland which is possibly *E. conicus* Kakudidi.

Pappophorum lindleyanum var. *pubescens* was wrongly labelled with the name and locality of var. *convolutum* (Burbidge 1941). Burbidge found that this specimen fitted Domin's description of var. *pubescens* and raised it to species level. She examined varieties *glaucum* and *laguroides* and found them to be similar to *E. nigricans* var. *barbinode*, which she described as *E. oblongus* N. Burb., sinking

varieties *glaucum* and *laguroides* into synonymy. However, present examination showed that *glaucum* and *laguroides* are distinct from *P. nigricans* var. *barbinode* as the latter represents *E. caerulescens*. Burbidge (1941) cited variety *scaberrimum* as a mixture of *E. pubescens* and *E. pallidus*, but the sheet at K bears only one specimen which is *E. pubescens*.

Under *P. nigricans* R. Br., Domin published 10 varieties, namely *Brownianum*, *glabrescens*, *robustissimum*, *arenicolum*, *pallidum*, *polyphyllum* with its form *plurinerve*, *purpurascens*, *pubiculme*, *gracile*, and *barbinode*. Variety *Brownianum* was *E. gracilis* (R. Br.) P. Beauv. except Brown's Keppel Bay specimen which Burbidge included under *E. arenicola* (Domin) N. Burb. Variety *glabrescens* Domin was found to be a mixture. Burbidge included the Winton specimen under *E. flavescens* (Lindl.) N. Burb.; the Jericho and Barcaldine specimens under *E. intermedius* N. Burb.; while Dempster's specimen from Frazer Range, Western Australia was included in *E. nigricans*. Evidently *E. intermedius* N. Burb. remained a mixture because she overlooked the specimens which she commented on as being near *E. gracilis*.

Varieties *robustissimum* and *arenicolum* Domin were raised to species level (Burbidge 1941). Variety *pallidum* was also a mixture. Robert Brown's specimen 6251 is the type for *E. pallidus* (R. Br.) P. Beauv. Burbidge included the specimen from Smelling Bluff, Chillagoe under *E. purpurascens* (R. Br.) P. Beauv., Dietrich 738 under *E. gracilis* (R. Br.) P. Beauv. She considered the rest of the material to belong to *E. polyphyllus* (Domin) N. Burb., that is, var. *polyphyllum* Domin. Form *plurinerve* was neglected as it was not represented.

Variety *purpurascens* Domin and var. *pubiculme* Domin were

found to represent *E. purpurascens* (R. Br.) P. Beauv. according to Burbidge (1941). However, present examination of var. *pubiculme* showed that it represented *E. pallidus*. Variety *gracile* Domin was raised to *E. gracilis* (R. Br.) P. Beauv. and var. *barbinode* Domin to *E. oblongus* N. Burb. (see above).

Under *Pappophorum avenaceum* Lindl. Domin listed 3 varieties, namely *typicum*, *depauperatum*, and *nanum*. According to Burbidge (1941) the first two were *E. avenaceus* (Lindl.) C. E. Hubb. and not distinct varieties, while var. *nanum* was included under *E. polyphyllus* (Domin) N. Burb., but present examination showed that var. *nanum* also represents *E. avenaceus*.

Hubbard (1937) described the next species *E. asperatus*. Burbidge (1941) described 6 new species, namely *E. intermedius*, *E. glaber*, *E. planifolius*, *E. clelandii*, *E. oblongus*, and *E. cylindricus* plus one variety *E. pallidus* var. *breviseta*. Changes in the delimitation of *E. intermedius* have been necessary as it was found to be a mixture. *E. glaber* N. Burb. and *E. planifolius* N. Burb. were sunk as taxonomic synonyms under *E. purpurascens*; while *E. pallidus* var. *breviseta* N. Burb. was sunk under *E. lindleyanus*; and *E. clelandii* N. Burb. was reduced to varietal status.

5.6. GENERIC DESCRIPTION

5.6.1. *Enneapogon* Desv. ex P. Beauv.

- *Enneapogon* Desv. ex P. Beauv., Ess. Agrostogr., 81 (1812); Desv., J.

Bot., 1: 70 (1813). - Type: Probably Argentina, Nee near Mendoza; ile Manilles was erroneously given as the locality according to Burbidge (1941), Chase (1946), and Hitchcock (1951).

- Pappophorum Schreb. auct. non *Trinius*, Fundamenta Agrostogr., 155 (1820); Kunth, Rev. Gram., 1: 82 (1829); *Trinius*, Mem. Acad. St. Petersb. ser. 6, Math. Phys. Nat., 1: 91 (1830).

Plants annual, or perennial, caespitose. Flowering culms erect to geniculate and ascending. Foliage and floral parts often with simple and stalked-glandular hairs. Mid-culm nodes hairy. Mid-culm internodes hairy to glabrous. Mid-culm sheaths hairy; the surface scabrous; rounded. Ligule ciliate. Collar hairy to glabrous. Mid-culm leaves flat to involute; linear to lanceolate; apices acuminate; the surface scabrous; margins serrulate.

Inflorescence a panicle; overall form of panicle contracted; branches terminating in a spikelet. Disarticulation of the spikelets above the glumes and tardily between the florets. Spikelets 3 to 8-flowered; with 1 to 3 fertile florets. Glumes equal or subequal in length; similar in texture (coriaceous or membranous); scabrous on main nerves; 4 to 24-nerved. Lower floret perfect. Lower lemma apically 9-nerved (rarely 10-16); chartaceous; ribbed, or not ribbed; usually hairy (glabrous in *E. polyphyllus* var. *denudatus*); pubescence on the lemma body villous with simple hairs; apically 9-awned; awns (when dry) straight or curved (neither twisted or kneed); usually subequal in length; plumose on the edges on the lower two-thirds and scabrous above; usually with a rim of cilia on the inner surface below the awns (lacking in *E. eremophilus*). Palea slightly longer than the lemma body; membranous; 2-nerved, the nerves pronounced and ciliolate. Lodicules present; well developed; 2 per floret; free; and cuneate.

Anthers 3 per floret; 0.4 to 2 mm long; yellow to purplish -pink. Styles 2 per floret; free; yellow to purplish-pink. Caryopses less than 3 mm long; the surface smooth; yellow to brown; compressed dorsiventrally. Embryo at least one-third as long as the caryopsis; constricted at about the middle in surface view. Second floret bisexual; or neuter (rarely male); glabrous or hairy; the upper florets neuter and often reduced to a few awns.

5.7. KEY TO THE SPECIES

KEY TO THE AUSTRALIAN ENNEAPOGON SPECIES

RBASE = 1.50, ABASE = 3.00, REUSE = 1.01, VARYWT = 0.80

CHARACTER MASK -

01022 45623 31052 67158 74507 37152 86606 33083 12001 20044 01554
60017 88764 30307 56070 97776 10432 43

- 1 (0). Apex of the palea of the lowest floret hairy 2
 - Apex of the palea of the lowest floret glabrous. 18
- 2 (1). Glume apices erose. 3
 - Glume apices not erose 14
- 3 (2). Spikelets with 1 fertile floret; lemma of the second floret glabrous. 4
 - Spikelets with 2 fertile florets; lemma of the second floret hairy on the lower part. E. intermedius

- 4 (3). Axillary inflorescence present.5
 Axillary inflorescence absent6
- 5 (4). Cleistogamous spikelets present in the axils of upper
 sheaths only; spikelets about same length throughout the
 panicle; branching concentrated on the upper nodes;
 spikelets ovate; surface of the body of the lowest lemma
 shallowly ribbedE. asperatus
- Cleistogamous spikelets present in the axils of the lower
 sheaths only; spikelets towards the panicle apex longer
 than those at the base; branching concentrated on the
 lower nodes; spikelets lanceolate; surface of the body of
 the lowest lemma deeply ribbed.E. caerulescens
- 6 (4). Leaf blades surfaces antrorsely scabrous. 7
 Leaf blades surfaces retrorsely scabrous. 11
- 7 (6). Leaf blades flat. E. pallidus
 Leaf blades involute. 8
- 8 (7). Leaf blades abaxially pilose.9
 Leaf blades abaxially glabrous10
- 9 (8). Glumes pilose; spikelets ovate; caryopsis 1.9 mm long or
 more; glumes not concealed by overlapping awns; mid-culm
 sheaths longer than their internodes (sheaths
 overlapping); glumes grey. . . . E. conicus var. clelandii
- Glumes glabrous; spikelets lanceolate; caryopsis up to 1.8
 mm long; glumes concealed by overlapping awns; mid-culm
 sheaths shorter than their internodes (sheaths not
 overlapping); glumes greenE. arenicola
- 10 (8). Spikelets ovate; surface of the body of the lowest lemma
 shallowly ribbed; internodes pilose.E. lindleyanus

- Spikelets lanceolate; surface of the body of the lowest lemma deeply ribbed; internodes villous . . . *E. conicus*
- 11 (6). Margins of the leaf blades antrorsely serrulate . . . 12
- Margins of the leaf blades retrorsely serrulate. . . . 13
- 12 (11). Leaf blades flat; leaf blades abaxially pilose.
- *E. pubescens*
- Leaf blades involute; leaf blades abaxially glabrous. . .
- *E. conicus*
- 13 (11). Glumes concealed by overlapping awns. . . . *E. robustissimus*
- Glumes not concealed by overlapping awns. . . . *E. pubescens*
- 14 (2). Hairs on the lowest lemma longer than the body. 15
- Hairs on the lowest lemma as long as the body. 16
- Hairs on the lowest lemma shorter than the body.
- *E. truncatus*
- 15 (14). Margins of the lowest lemma ciliate; awn bases lacking a thickened ridge; surface of the body of the lowest lemma ribbed on the upper part; body of the lowest lemma lacking marginal hyaline lobes; leaf blades abaxially glabrous . .
- *E. intermedius*
- Margins of the body of the lowest lemma glabrous; awn bases with a thickened ridge; surface of the body of the lowest lemma not ribbed; body of the lowest lemma normally with marginal hyaline lobes; leaf blades abaxially pilose . .
- *E. avenaceus*
- 16 (14). Body of the lowest lemma hairy all over; plants annual. . .
- *E. virens*
- Body of the lowest lemma hairy on the lower part; plants perennial 17

- 17 (16). Margins of the body of the lowest lemma ciliate; awn bases
lacking a thickened ridge; glumes grey. . . .E. nigricans
Margins of the body of the lowest lemma glabrous; awn bases
with a thickened ridge; glumes green.E. gracilis
- 18 (1). Spikelets with 1 fertile floret; lemma of the second
floret glabrous. 19
Spikelets with 2 fertile florets; lemma of the second
floret hairy on the lower part. 26
- 19 (18). Hairs on the lowest lemma longer than the body. 20
Hairs on the lowest lemma as long as the body. 21
Hairs on the lowest lemma shorter than the body. 24
- 20 (19). Glume apices erose; axillary inflorescence present; margins
of the body of the lowest lemma ciliate; flowering culms
disarticulating at the nodes; sterile florets not crowded
distally; sterile florets not reflexed. . . .E. cylindricus
Glume apices not erose; axillary inflorescence absent;
margins of the body of the lowest lemma glabrous;
flowering culms not disarticulating at the nodes; sterile
florets crowded distally; sterile florets reflexed
.E. polyphyllus
- 21 (19). Leaf blade apices hair-likeE. purpurascens
Leaf blade apices not hair-like 22
- 22 (21). Body of the lowest lemma dorsally convex; spikelets
lanceolate; body of the lowest lemma lacking extra nerves
between the main ones. 23
Body of the lowest lemma dorsally straight; spikelets
ovate; body of the lowest lemma with extra nerves between
the main ones.E. oblongus

23 (22). Axillary inflorescence present; palea of the lowest floret hairy between the nerves; palea of the lowest floret hairy on the flaps; leaf blades involute; flowering culms disarticulating at the nodes E. cylindricus

Axillary inflorescence absent; palea of the lowest floret glabrous between the nerves; palea of the lowest floret glabrous on the flaps; leaf blades flat; flowering culms not disarticulating at the nodesE. eremophilus

24 (19). Body of the lowest lemma hairy on the lower part; margins of the body of the lowest lemma ciliate; sterile florets not reflexed; sterile florets not crowded distally; leaf blades flat.25

Body of the lowest lemma glabrous (except for a hair tuft at the base); margins of the body of the lowest lemma glabrous; sterile florets reflexed; sterile florets crowded distally; leaf blades involute.
. E. polyphyllus var. denudatus

25 (24). Leaf blade apices hair-like; palea of the lowest floret hairy on the flaps; inner rim of cilia present below the awns. E. purpurascens

Leaf blade apices not hair-like; palea of the lowest floret glabrous on the flaps; inner rim of cilia absent below the awns. E. eremophilus

26 (18). Leaf blade apices hair-like; body of the lowest lemma dorsally convex; palea of the lowest floret glabrous between the nerves; rachilla between the lower two florets without a hair tuft; leaf blades abaxially pilose. . . .
. E. decipiens

Leaf blade apices not hair-like; body of the lowest lemma dorsally straight; palea of the lowest floret hairy between the nerves; rachilla between the lower two florets with a hair tuft; leaf blades abaxially glabrous. . . . 27

27 (26). Hairs on the lowest lemma longer than the body; spikelets towards the apex of the panicle longer than those at the base; body of the lowest lemma lacking extra nerves between the main ones; awns 5.2 mm long or more; upper glume 5.1 mm long or more.

. *E. caerulescens* var. *occidentalis*

Hairs on the lowest lemma as long as the body; spikelets about the same length throughout the panicle; body of the lowest lemma with extra nerves between the main ones; awns up to 5.1 mm long; upper glume up to 5 mm long.

. *E. oblongus* var. *papposus*

5.8. TAXONOMIC TREATMENT

5.8.1. *E. avenaceus*

E. avenaceus (Lindl.) C. E. Hubb.

(1) *E. avenaceus* (Lindl.) C. E. Hubb., Kew Bull., 1934: 450 (1934). -
in T. L. Mitchell, (1848)
Pappophorum avenaceum Lindl., J. Exped. Trop. Austral., 320. - Type:
Queensland, Mitchell District, N. W of Blackall on Victoria River (now
known as Barcoo River) in 24° 1' S 145° 2' E, collected on 22

September 1848, T. L. Mitchell s.n CGE !.

- *Pappophorum avenaceum* var. *typicum* Domin, *Biblioth. Bot.*, 20: 383 (1915), based on *P. avenaceum* Lindl. s. str.; Domin's specimen was from Queensland, Rolling Downs, collected in March 1910. - Holotype: PR, n.v; isotype: K !.

- *P. avenaceum* var. *depauperatum* Domin , *Biblioth Bot.*, 20: 383 (1915). - Type: South Australia, in the vicinity of Lake Eyre, Andrews 69, K, n.v.

- *P. avenaceum* var. *nanum* Domin, *Biblioth. Bot.*, 20: 383 (1915). - Type: Queensland, Cloncurry, collected in February 1910, Domin s.n. - Holotype: PR, n.v; isotype: K !.

(2) Plants annual to perennial; (3) caespitose. (4) Flowering culms 10 to 45 cm tall (average 25.7); (5) erect, or geniculate and ascending (rare); (6) branched; (8) not disarticulating at the nodes; (9) nodes hairy; (10) internodes pilose. (11) Mid-culm sheaths longer than their internodes (sheaths overlapping), or shorter than their internodes (sheaths not overlapping); (12) hairy. (13) Ligule 0.4 to 1.2 mm long (average 0.9). (14) Leaf blades 4.4 to 14.7 cm long (average 7.9); (15) 1.2 to 6 mm wide (average 3.3); (16) flat to involute; (17) surface antrorsely scabrous; (18) adaxially pilose; (19) abaxially pilose; (20) apices not hair-like; (21) margins antrorsely serrulate. (22) Inflorescence 3.1 to 9.7 cm long (average 5.7); (23) loosely contracted; (24) ovate to lanceolate; (25) axillary inflorescence absent. (27) Spikelets about the same length throughout the panicle; (28) 5.7 to 19.6 mm long (average 11.5); (29) lanceolate; (30) 3 to 4-flowered; (31) with 2 fertile florets; (32) sterile florets not crowded distally; (33) sterile florets not reflexed. (34) Glumes subequal; (35) pilose; (36) coriaceous; (37) green to grey;

(38) margins pale green to purplish; (39) apices not erose; (40) not concealed by overlapping awns. (41) Lower glume 4.5 to 12 mm long (average 7.5); (42) 11 to 23-nerved (frequently 16-22); (43) obtuse to acute; (44) lanceolate to ovate. (45) Upper glume 4.7 to 13.6 mm long (average 8.7); (46) 8 to 19-nerved (frequently 13-19); (47) obtuse to acute; (48) lanceolate to ovate. (49) Body of the lowest lemma 2.1 to 3.5 mm long (average 2.8); (50) 1.8 to 4.8 mm wide (average 3.4); (51) apex truncate to apex obtuse; (52) 9 to 11 -nerved; (53) lacking extra nerves between main ones; (54) 1 to 2 nerve(s) entering each peripheral awn; (56) surface not ribbed; (57) papillose; (58) yellow to grey; (60) dorsally convex; (61) hairy on the lower part; (62) hairs longer than the body; (63) margins glabrous; (64) normally with marginal hyaline lobes. (65) Body width to the length 1 to 1.5 (average 1.3). (66) Body length to the length of awns 0.2 to 0.6 (average 0.3). (67) Awns 9; (68) 3.8 to 15.4 mm long (average 8.9); (69) subequal; (70) bases with a thickened ridge; (71) yellow to grey; (72) inner rim of cilia present. (73) Palea of the lowest floret 2.2 to 5.2 mm long (average 3.8); (74) hairy between the nerves; (75) apex cleft; (76) apex hairy; (77) hairy on the flaps. (78) Rachilla between lower two florets without a hair tuft. (79) Lemma of the second floret not ribbed; (80) hairy on the lower part. (81) Anthers 0.4 to 1.6 long (average 0.7); (82) yellow. (83) Caryopsis 1.5 to 2.5 mm long (average 1.9); (84) 1 to 1.9 mm wide (average 1.6); (85) globoid to ellipsoid. (86) Embryo 0.5 to 1 the caryopsis length (average 0.8); (87) 1 to 2.1 mm long (average 1.6).

Affinities: The close relatives are *E. gracilis* and *E. virens* but it differs from them by having a lemma with hairs that are longer than the body and with hyaline lobes on the margins.

Distribution: Occurs in all states except Victoria and Tasmania. (Map 1)

Ecology: The species occurs in vegetation communities ranging through arid and semi-arid woodlands, arid tussock and hummock grasslands, and shrublands of *Eucalyptus* (Mallee) and *Acacia* and shrub steppe (Moore 1970). According to collectors' notes, associated species include *Eucalyptus terminalis*, *Acacia* spp., *A. sowdenii*, *Cassia* spp., *Owenia* sp., *Casuarina aristata*, *Hakea divaricata*, *Aristida* spp., *Maireana aphylla*, *Astrebla pectinata* and *A. lappacea*. The soils range from deep red fine sandy loams to yellow brown silty loams, dark brown loams, clays and outcrops of limestone boulders.

Representative specimens (40/525)

NEW SOUTH WALES: along road between Tero Creek station and White Cliffs, Martensz CANB 201316 (CANB); 11.5 km S. of Tilpa road, E. of Darling River, Moore 7242 (CANB); Quarry View, 7 miles S. of Bootra, Vasek 680731-35 (CANB); Mount Mulyah, Moore 5806, 5815, 5813, 5817, 5213, 5814 (CANB); Tundulyah, Moore 5581, 4889 (CANB); Bourke township, McBarron 14650 (BRI); Yantara creek, Chinnock 3407 (AD); Quondong Vale station, Eichler 21550 (AD); Darling River, Herbarium Tate AD 97609602 (AD).

NORTHERN TERRITORY: 14 miles S. of Erldunda Homestead, Winkworth 135 (BRI CANB); 18 miles S. E of Tempe Downs Homestead, Winkworth 42 (BRI CANB); Mount Gillen, Pullen 10455 (CANB); Supplejack Homestead airstrip, Latz 7928 (CANB); 26 miles N. of Georgina Downs Homestead, Latz 1685 (AD BRI CANB); S. of L. Neale, Latz 2431 (CANB); Todd River, 26 miles E. S. E of Alice Springs, Nelson 1859 (BRI CANB); Andado, Buckley 1682 (CANB).

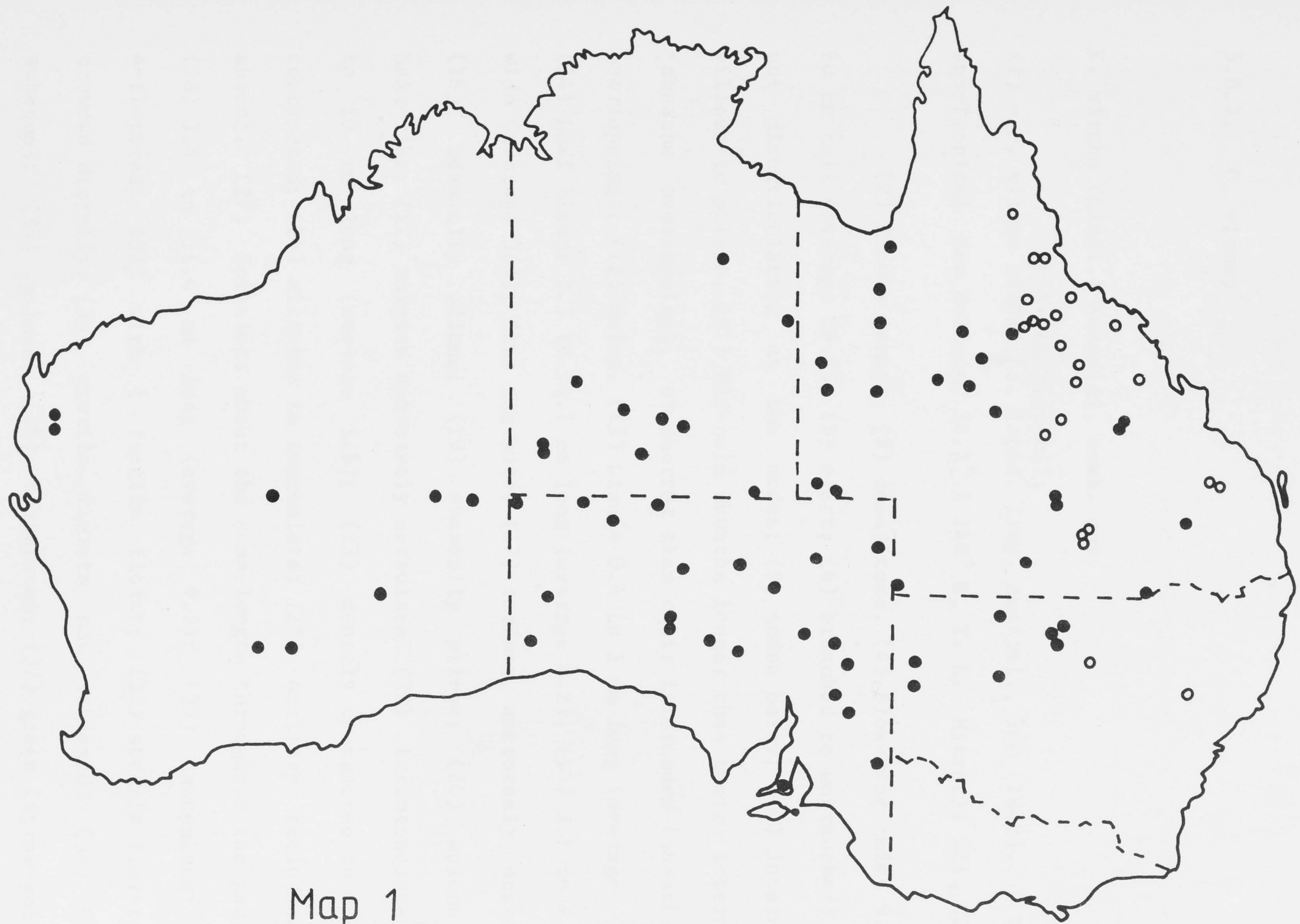
QUEENSLAND: Marathon station, W. of Hughenden, Hubbard & Winders 7753 (BRI CANB); 40 miles N. W of Cloncurry, 7 to 8 miles W. of Naraku, Beaumont 7067A (CANB); Cloncurry, Hubbard 7313 (BRI CANB); 15 miles W. of Morestone, Perry 985 (CANB); Mount Isa, Winders 7387 (BRI CANB); Nonda, Hubbard & Winders 7241 (BRI CANB); between Amby and Eurella, Hubbard & Winders 6372 (CANB); 30 km W. of St. George, Blake 10812 (BRI); Prairie, Hubbard & Winders 7068 (CANB); 8 km N. E of Dajarra township, Lazarides 4354 (BRI CANB); Birdsville, Boyland 168 (BRI); Fairbairn Dam, Simon 2894B (BRI); 51 km N. of Charleville on Augathella road, Purdie & Boyland 166 (BRI CANB).

SOUTH AUSTRALIA: 126 km N. of Cook, Symon 12712 (CANB); Motpena station, east shore of L. Torrens, Ogden ANU 18103 (CANB); S. of Wartaloona, 25 km S. of Balcanoona, Whibley 4107 (AD CANB); 3 km S. of Monash, Eichler 13723 (AD); Muloorina station, Hill 235 (AD).

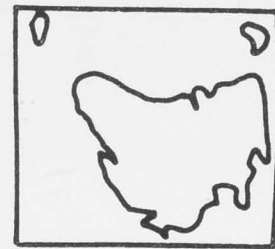
WESTERN AUSTRALIA: Wongawall creek, Speck 1288 (CANB); northern end of Cavernah Range, George 4776 (PERTH); 5 km W. of Coolgardie, Hacker s.n 3. iii. 1971 (PERTH); 2 miles W. of Warburton Mission, George 3808 (PERTH); Giles Camp area, 7 km S. of Giles, Kuchel 189 (AD);

References: Bailey (1902); Black (1978: 185); Burbidge (1941: 63, fig. 1); Cameron (1979: 159, fig. 51); Cunningham et al. (1981: 93, fig. 20a); Gardner (1952: 30); Jacobs & Pickard (1981: 41); Jessop (1981: 454, fig. 508A); Lazarides (1970: 118, pl. 33a); Maiden (1898b: 142); Maiden & Betche (1916: 7); Turner (1895: 44, fig. on opposite page); Turner (1893: 414); Vickery (1953: 84); Willis (1970: 168).

Map 1. Distribution of *E. avenaceus* (●) and *E. virens* (o).



Map 1



5.8.2. *E. virens*

E. virens (Lindl.) Kakudidi, comb. nov.

in T. L. Mitchell,

(1) - *P. virens* Lindl., J. Exped. Trop. Austral., 360 (1848). - Type:
Sub-Tropical New Holland, 26.2° S 148° E, T. L. Mitchell 521, CGE !.

(2) Plants annual; (3) caespitose. (4) Flowering culms 9.5 to 60 cm tall (average 29.4); (5) erect; (6) branched to unbranched; (8) not disarticulating at the nodes; (9) nodes hairy; (10) internodes villous to pilose. (11) Mid-culm sheaths longer than their internodes (sheaths overlapping), or shorter than their internodes (sheaths not overlapping); (12) hairy. (13) Ligule 0.4 to 1 mm long (average 0.8). (14) Leaf blades 2.5 to 14.7 cm long (average 8.2); (15) 2.1 to 4.5 mm wide (average 3.2); (16) involute; (17) surface antrorsely scabrous; (18) adaxially pilose; (19) abaxially pilose; (20) apices not hair-like; (21) margins antrorsely serrulate. (22) Inflorescence 1.6 to 10 cm long (average 5.5); (23) densely contracted to loosely contracted; (24) elliptic to lanceolate; (25) axillary inflorescence absent. (27) Spikelets about the same length throughout the panicle; (28) 3.4 to 11.4 mm long (average 9.3); (29) lanceolate; (30) 4-flowered; (31) with 1 fertile floret; (32) sterile florets not crowded distally; (33) sterile florets not reflexed. (34) Glumes subequal; (35) pilose; (36) coriaceous; (37) green (straw-coloured when mature); (38) margins pale green; (39) apices not erose; (40) not concealed by overlapping awns. (41) Lower glume 4 to 7.4 mm long

(average 5.2); (42) 6 to 11-nerved (frequently 7-9); (43) acute to acuminate; (44) lanceolate to ovate. (45) Upper glume 3.9 to 8.2 mm long (average 5.5); (46) 5 to 8-nerved (frequently 7); (47) acute to acuminate; (48) lanceolate to ovate. (49) Body of the lowest lemma 2 to 3.8 mm long (average 2.5); (50) 2.2 to 4 mm wide (average 3.4); (51) apex truncate to apex obtuse; (52) 9-nerved (rarely 11-nerved); (53) lacking extra nerves between main ones; (54) 1 nerve entering each peripheral awn; (56) surface not ribbed; (57) papillose; (58) yellow; (60) dorsally convex; (61) hairy all over; (62) hairs as long as the body; (63) margins ciliate; (64) lacking marginal hyaline lobes. (65) Body width to the length 1 to 1.8 (average 1.2). (66) Body length to the length of the awns 0.3 to 0.5 (average 0.4). (67) Awns 9; (68) 4.8 to 9 mm long (average 7.1); (69) subequal; (70) bases with a thickened ridge; (71) yellow to grey; (72) inner rim of cilia present. (73) Palea of the lowest floret 2.5 to 3.2 mm long (average 2.8); (74) hairy between the nerves; (75) apex cleft; (76) apex hairy; (77) hairy on the flaps. (78) Rachilla between lower two florets without a hair tuft. (79) Lemma of the second floret not ribbed; (80) glabrous. (81) Anthers 0.8 to 1 mm long (average 0.9); (82) yellow to purplish-pink. (83) Caryopsis 1.6 to 1.9 mm long (average 1.8); (84) 1.2 to 1.4 mm wide (average 1.3); (85) globoid to ellipsoid. (86) Embryo 0.7 to 0.9 the caryopsis length (average 0.8); (87) 1.3 to 1.6 mm long (average 1.4).

Remarks: The type is a small specimen about 12 cm tall with deep green leaves, although most of the material examined is more than 20 cm tall. Burbidge (1941) commented on the specimen as a small rigid form of *E. gracilis* and not a distinct species.

Affinities: The species is closely related to *E. gracilis*, but it differs in having the body of the lemma hairy all over.

Distribution: New South Wales and Queensland. (Map 1)

Ecology: The species occurs mainly in tropical and sub-tropical woodlands, semi-arid shrub woodlands, and brigalow forests (Moore 1970). Associated species include *Eucalyptus peltata*, *E. polycarpa*, *E. papuana*, *E. melanophloia*, *E. cullenii*, *Acacia bidwillii*, *A. excelsa*, *Erythrophleum chlorostachyum*, *Planchonia careya*, *Digitaria gibbosa*, *Brachiaria holosericea*, *Alloteropsis cimicina*, *Rottboellia formosa* and *Enneapogon* spp. Soils range from siliceous sands, and other sandy soils by river banks, red sands to red-brown sandy loams.

Representative specimens (14/24)

NEW SOUTH WALES: Boppy Mountains, between Nyngan and Borah, Moore 7631 (CANB); Goulburn River, 20 miles W. of Merriwa, Hunter Valley, Story 7028 (CANB); no specific locality, sub-tropical New Holland, Mitchell s.n. 1846 (CGE).

QUEENSLAND: 12 miles S. W. of Martina station, Adams 1159 (CANB); 3 miles N. of Moray Downs station, Adams 1176 (CANB); Oakvale, Rich BRI 266945 (BRI); Burdekin crossing near Glendon, Smith 4588 (BRI); Boatman station, Everist 2814 (CANB); near source of Poison creek, N. of Hughenden, Blake 8575A (CANB); 4 miles E. of Lucy Hut on road leading to Oak Hill, Morain 137 (BRI); near Pentland, Blake 6139 (BRI); Erne, 45 miles E. N. E of Blackall, Everist 1813 (BRI); Epping Forest National Park near Clermont, Wilkinson A35 (BRI); Broomsound Shire, New Bombandry, 80 km S. of Nebo, Anderson 877 (BRI).
References: Burbidge (1941: 66); Cameron (1979: 169); Cunningham et

al. (1981: 95); Jacobs & Pickard (1981: 44); Vickery (1953: 84), all cited as *E. gracilis*.

5.8.3. *E. gracilis*

E. gracilis (R. Br.) P. Beauv.

Fig. 1.

(1) *E. gracilis* (R. Br.) P. Beauv., Ess. Agrostogr., 82 & 162 (1812); Desv., J. Bot., 1: 70 (1813). - *Pappophorum gracile* R. Br., Prod., 185 (1810). - Type: Queensland, Broad Sound R. Brown 6252. - Holotype: BM, n.v; isotype: K !.

(2) Plants perennial; (3) caespitose. (4) Flowering culms 12.5 to 70 cm tall (average 41.0); (5) erect; (6) branched; (8) not disarticulating at the nodes; (9) nodes hairy; (10) internodes pilose. (11) Mid-culm sheaths shorter than their internodes (sheaths not overlapping); (12) hairy to glabrous. (13) Ligule 0.4 to 0.8 mm long (average 0.6). (14) Leaf blades 3.5 to 11.5 cm long (average 8.1); (15) 2 to 3.8 mm wide (average 3.0); (16) flat to involute; (17) surface antrorsely scabrous; (18) adaxially pilose; (19) abaxially pilose; (20) apices not hair-like; (21) margins antrorsely serrulate. (22) Inflorescence 1.8 to 7.5 cm long (average 4.2); (23) loosely contracted; (24) elliptic, or lanceolate to linear; (25) axillary inflorescence absent. (27) Spikelets about the same length throughout the panicle; (28) 6 to 11 mm long (average 9.4); (29) ovate to lanceolate; (30) 3 to 6-flowered; (31) with 1 fertile floret; (32) sterile florets not crowded distally; (33) sterile florets not

reflexed. (34) Glumes subequal; (35) pilose; (36) coriaceous; (37) green (straw-coloured on maturing); (38) margins pale green; (39) apices not erose; (40) not concealed by overlapping awns. (41) Lower glume 4 to 7 mm long (average 5.4); (42) 6 to 15-nerved (frequently 7-11); (43) acute to acuminate; (44) lanceolate to ovate. (45) Upper glume 4.3 to 8.8 mm long (average 6.6); (46) 5 to 11 -nerved; (47) acute to acuminate; (48) lanceolate to ovate. (49) Body of the lowest lemma 2.2 to 3.1 mm long (average 2.6); (50) 2.4 to 3.8 mm wide (average 3.2); (51) apex truncate; (52) 9 to 11-nerved; (53) lacking extra nerves between main ones; (54) 1 to 2 nerve(s) entering each peripheral awn; (56) surface ribbed on the upper part, or not ribbed; (57) papillose; (58) yellow to grey; (60) dorsally convex; (61) hairy on the lower part; (62) hairs as long as the body; (63) margins glabrous; (64) lacking marginal hyaline lobes. (65) Body width to the length 1 to 1.7 (average 1.3). (66) Body length to the length of the awns 0.3 to 0.9 (average 0.4). (67) Awns 9; (68) 3 to 9 mm long (average 6.6); (69) subequal; (70) bases with a thickened ridge; (71) yellow to grey; (72) inner rim of cilia present. (73) Palea of the lowest floret 2.6 to 3.6 mm long (average 3.0); (74) hairy between the nerves; (75) apex cleft; (76) apex hairy; (77) hairy on the flaps. (78) Rachilla between lower two florets without a hair tuft. (79) Lemma of the second floret not ribbed; (80) glabrous. (81) Anthers 0.8 to 1.5 mm long (average 1.0); (82) yellow to purplish-pink. (83) Caryopsis 1.5 to 1.8 mm long (average 1.6); (84) 1.1 to 1.4 mm wide (average 1.3); (85) globoid to ellipsoid. (86) Embryo 0.7 to 0.9 the caryopsis length (average 0.8); (87) 0.9 to 1.4 mm long (average 1.0).

Remarks: The species was included in *Pappophorum nigricans* R. Br. by Bentham, Fl. Austral., 7: 600 (1878) and reduced to *P. nigricans* var.

gracile Domin, Biblioth. Bot., 20: 382 (1915) based on Brown 6252. Domin's specimen was from Charters Towers, collected in February 1910. Burbidge included some of the material belonging to this species under *E. intermedius*. She described the lemma of *E. intermedius* as 'short and broad, truncate at the apex as in the two preceding species,....' implying *E. avenaceus* and *E. gracilis*. This description agrees with the lemma of *E. gracilis* rather than *E. intermedius* and therefore the two are distinct species.

Affinities: The species is closely related to *E. virens*, but it differs in having a partly hairy lemma with glabrous margins in contrast to the entirely hairy lemma of *E. virens*.

Distribution: Queensland and New South Wales. (Map 2a)

Ecology: The species occurs mainly in tropical and sub-tropical and temperate woodlands, semi-arid shrub woodlands, and brigalow forests (Moore 1970). Associated species include *Eucalyptus populnea*, *E. dichromophloia*, *E. crebra*, *Acacia harpophylla*, *A. excelsa*, *Bothriochloa decipiens*, *B. bladhii*, *Heteropogon* sp., *Themeda australis*, *Aristida* spp., *Stipa setacea*. The soils range from sandy loams to sandy alluvium, fine textured clays to basaltic rocks on hill slopes.

Representative specimens (22/30)

NEW SOUTH WALES: 10 miles W. of Singleton, Story 7136 (CANB); Fiddlers creek near Tomingley, Pullen & Galore 4671 (CANB); western outskirts of Rouchel Brook, Story 7108 (CANB); 26 miles S. W of Denman, Story 6777 (CANB); 2 miles S. W of Delgate River - Snowy River junction, Wimbush 241 (CANB); Boggabilla, Winders BRI 287076 (BRI).

QUEENSLAND: Emu Plains, 64 miles N. of Hughenden, Hubbard & Winders 7545 (BRI CANB); Mungallala, Hubbard & Winders 6031 (BRI CANB), 6066 (BRI); S. W of Cooroorah Homestead, Story & Yapp 195 (BRI CANB); N. E of Clerke River township, Lazarides 4651 (CANB); Kangaroo Hill station, N. W of Townsville, Lazarides 7125 (CANB); Drayton, Blake 5170 (BRI); between Pittsworth & Milmerran, White 10053 (BRI); Augathella, White 11672 (BRI); 2 miles S. W of Glen Avon station, Adams (BRI CANB); Callide Cotton Research Station, Cowdry 64 (BRI); near Lindley, Blake 10417 (BRI); Roma, White 9582 (BRI); Dirranbandi, Blake 10606A (BRI); Curragh, N. of Blackwater, Johnson 2861 (BRI); Emerald, Finlay & Farquhar 10 (BRI); Dingo, between Emerald and Rockhampton, Hubbard 8017 (BRI).

References: Tothill (1973: 149, fig. on p. 148); Tothill & Hacker (1983: 221, fig. on p. 220).

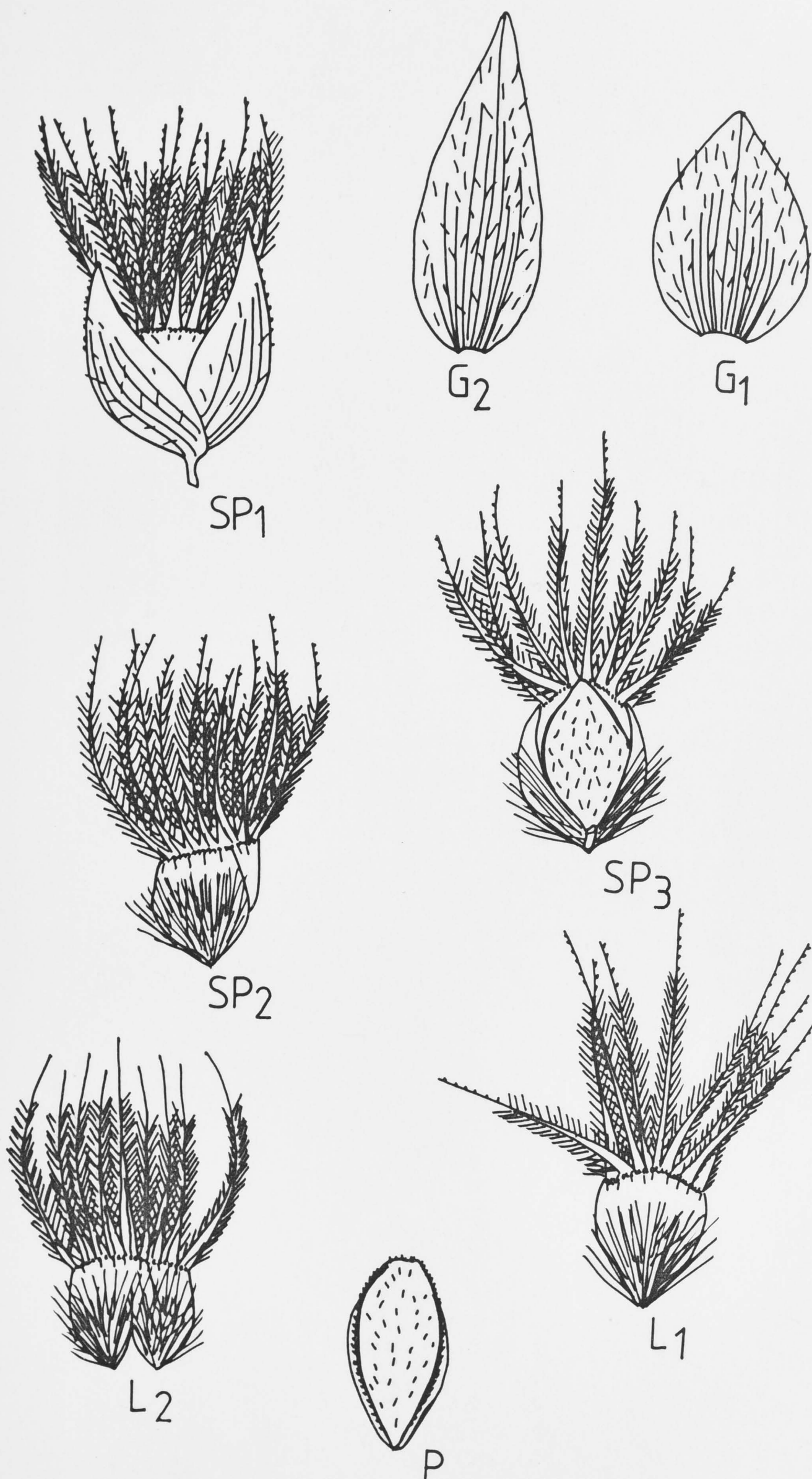


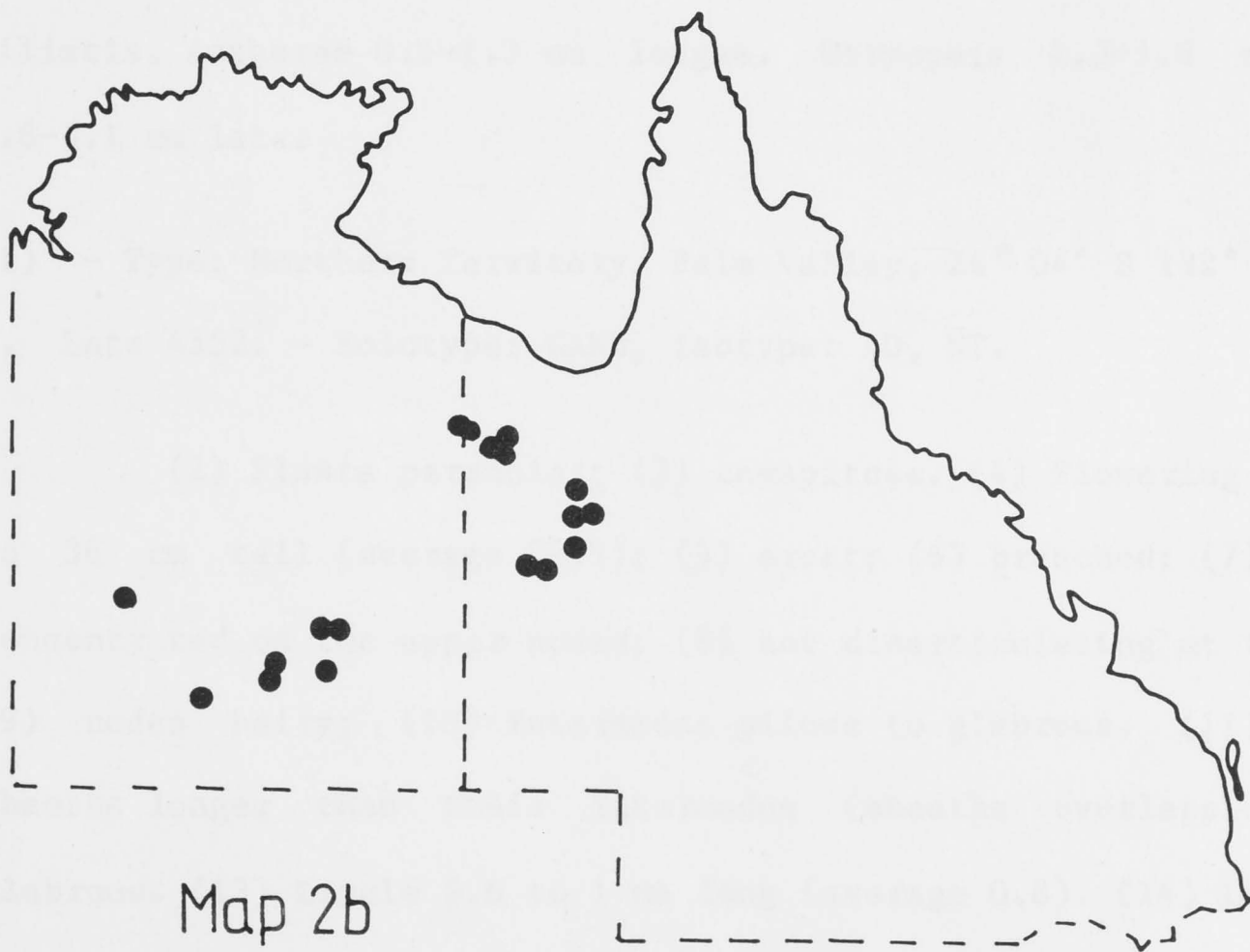
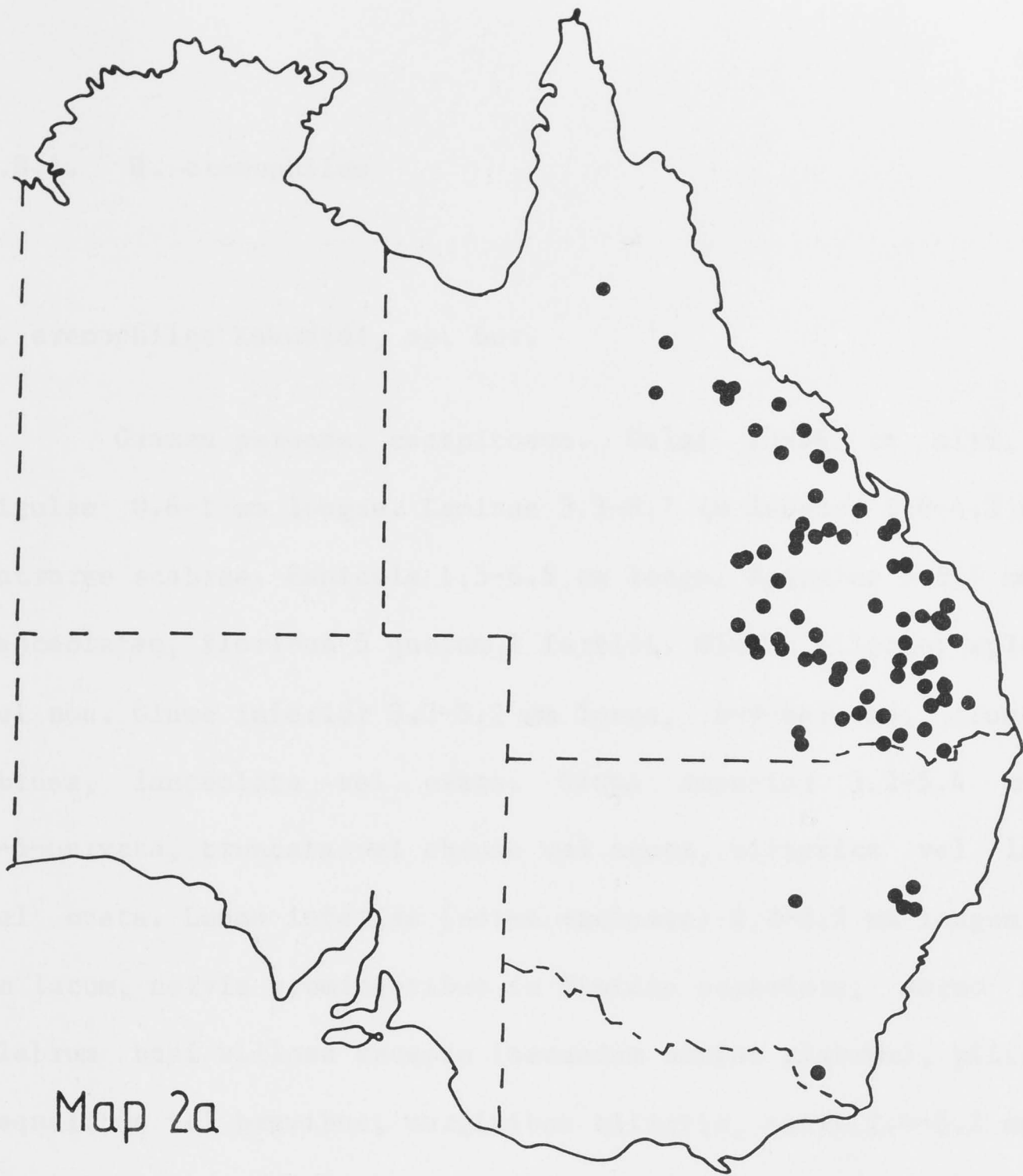
Fig. 1. *E. gracilis*

SP1, spikelet; SP2, SP3, florets; G1, lower glume; G2, upper glume;
P, palea; L1, L2, lower lemma.

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Map 2a. Distribution of *E. gracilis*.

Map 2b. Distribution of *E. eremophilus*.



5.8.4. *E. eremophilus*

E. eremophilus Kakudidi, sp. nov.

Gramen perenne, caespitosum. Culmi 13-36 cm alti, erecti. Ligulae 0.6-1 mm longae. Laminae 3.3-8.7 cm longae, 1.6-4.2 mm latae, antrorse scabrae. Panicula 1.5-6.5 cm longa. Spiculae 5-8.5 mm longae, lanceolatae, floribus 5 quorum 1 fertili. Glumae pilosae; apices erosi vel non. Gluma inferior 3.2-5.2 mm longa, 6-9-nervata, truncata vel obtusa, lanceolata vel ovata. Gluma superior 3.2-5.4 mm longa, 4-5-nervata, truncata vel obtusa vel acuta, elliptica vel lanceolata vel ovata. Lemma inferius (setae exclusae) 2.2-3.5 mm longum, 1.8-2.8 mm latum, nervis prominentibus in dimidio superiore, dorso convexum, glabrum basi villosa excepta (secundum omnino glabrum), pilis lemmate aequalibus vel brevibus, marginibus ciliatis, setis 2.4-5.2 mm longis, ad basim interiora glabra. Palea 2.2-3.8 mm longa, glabra, nervis ciliatis. Antherae 0.6-1.3 mm longae. Caryopsis 1.3-1.8 mm longa, 0.8-1.1 mm lata.

(1) - Type: Northern Territory, Palm Valley, 24° 04' S 132° 42' E, P. K. Latz 4352. - Holotype: CANB, isotype: AD, NT.

(2) Plants perennial; (3) caespitose. (4) Flowering culms 13 to 36 cm tall (average 26.5); (5) erect; (6) branched; (7) branches concentrated on the upper nodes; (8) not disarticulating at the nodes; (9) nodes hairy; (10) internodes pilose to glabrous. (11) Mid-culm sheaths longer than their internodes (sheaths overlapping); (12) glabrous. (13) Ligule 0.6 to 1 mm long (average 0.8). (14) Leaf blades 3.3 to 8.7 cm long (average 6.4); (15) 1.6 to 4.2 mm wide (average

3.0); (16) flat; (17) surface antorsely scabrous; (18) adaxially pilose; (19) abaxially glabrous; (20) apices not hair-like; (21) margins antorsely serrulate. (22) Inflorescence 1.5 to 6.5 cm long (average 2.7); (23) loosely contracted; (24) lanceolate; (25) axillary inflorescence absent. (27) Spikelets about the same length throughout the panicle; (28) 5 to 8.5 mm long (average 6.6); (29) lanceolate; (30) 5-flowered; (31) with 1 fertile floret; (32) sterile florets not crowded distally; (33) sterile florets not reflexed. (34) Glumes subequal; (35) pilose; (36) coriaceous; (37) green (straw-coloured on maturing); (38) margins purplish; (39) apices erose, or not erose; (40) not concealed by overlapping awns. (41) Lower glume 3.2 to 5.2 mm long (average 4.1); (42) 6 to 9-nerved; (43) truncate to obtuse; (44) lanceolate to ovate. (45) Upper glume 3.2 to 5.4 mm long (average 4.2); (46) 4 to 8-nerved (frequently 5); (47) truncate to acute, or mucronate; (48) elliptic, or lanceolate to ovate. (49) Body of the lowest lemma 2.2 to 3.5 mm long (average 3.0); (50) 1.8 to 2.8 mm wide (average 2.4); (51) apex obtuse (prominently so); (52) 9-nerved; (53) lacking extra nerves between main ones; (54) 1 nerve entering each peripheral awn; (56) surface ribbed on the upper part; (57) smooth; (58) yellow; (60) dorsally convex; (61) hairy on the lower part; (62) hairs as long as, to hairs shorter than, the body; (63) margins ciliate; (64) lacking marginal hyaline lobes. (65) Body width to the length 0.7 to 1.1 (average 0.8). (66) Body length to the length of the awns 0.4 to 1.2 (average 0.7; the body often longer than awns). (67) Awns 9; (68) 2.4 to 5.2 mm long (average 3.9); (69) shorter than mid-awn; (70) bases lacking a thickened ridge; (71) purplish-pink; (72) inner rim of cilia absent. (73) Palea of the lowest floret 2.2 to 3.8 mm long (average 2.8); (74) glabrous between

the nerves; (75) apex cleft; (76) apex glabrous; (77) glabrous on the flaps. (78) Rachilla between lower two florets without a hair tuft. (79) Lemma of the second floret not ribbed; (80) glabrous. (81) Anthers 0.6 to 1.3 mm long (average 0.9); (82) purplish-pink. (83) Caryopsis 1.3 to 1.8 mm long (average 1.7); (84) 0.8 to 1.1 mm wide (average 1.0); (85) obovoid to ellipsoid. (86) Embryo 0.6 to 0.9 the caryopsis length (average 0.8); (87) 1.1 to 1.6 mm long (average 1.3).

Affinities: The species is closely related to *E. decipiens* but it differs in having a lemma that has a prominently obtuse apex and lacks an inner rim of cilia, one fertile floret per spikelet, the second lemma glabrous, and a palea which is always glabrous between the nerves and on the flaps.

Distribution: Northern Territory and Queensland. (Map 2b)

Ecology: It occurs mainly in shrub steppe and Acacia shrublands, arid tussock and hummock grasslands (Moore 1970), also Eucalyptus woodlands with the ground cover of hummock grasses.

Representative specimens (10/18)

NORTHERN TERRITORY: Palm Valley, Latz 4352 (AD CANB), Ringwood station, Latz 4447 (CANB); 20 miles N. N. E of Huckitta Homestead, Latz 671, 1097 (CANB); Carrara creek, Latz 1663 (BRI CANB); Mappata water hole, 20 miles N. N. E. of Huckitta Homestead, Perry 986 (CANB); Mount Benstead creek, Latz 1946 (AD BRI CANB); Mount Doreen station, Latz 2032 (BRI).

QUEENSLAND: 15 miles W. of Morestone station, Perry 986 (BRI CANB); River Sleigh, Blake 8656 (BRI); Corella Range crossing, 46 miles W. S. W of Cloncurry, Henderson H1877 (BRI).

References: Burbidge (1941: 69); Jessop (1981: 454), all as *E. purpurascens*.

5.8.5. *E. purpurascens*

E. purpurascens (R. Br.) P. Beauv.

(1) *E. purpurascens* (R. Br.) P. Beauv., Ess. Agrostogr., 82 & 161 (1812) ; Desv., J. Bot., 1: 70 (1813). - *P. purpurascens* R. Br., Prod., 185 (1910). - Type: Queensland, Gulf of Carpentaria, R. Brown 6250. - Holotype: BM, n.v; isotype: K !.

- *P. nigricans* var. *purpurascens* (R. Br.) Domin Biblioth. Bot., 20: 382 (1915), - Type: Islands of the Gulf of Carpentaria, R. Brown 6250.

- *E. glaber* N. Burb., Proc. Linn. Soc. Lond., 153: 72 (1941). - Type: Western Australia, East Kimberley District, F. Connor 12, PERTH !.

- *E. planifolius* N. Burb., Proc. Linn. Soc. Lond., 153: 73 (1941). -Type: Western Australia, West Kimberley, Noonkanbah station, Station Manager s.n (N. T. Burbidge K333) PERTH !.

(2) Plants annual to perennial (short-lived); (3) caespitose. (4) Flowering culms 6 to 75 cm tall (average 38.4); (5) erect; (6) branched; (8) not disarticulating at the nodes; (9) nodes hairy; (10) internodes glabrous (except near the nodes). (11) Mid-culm sheaths longer than their internodes (sheaths overlapping), or shorter than their internodes (sheaths not overlapping); (12) hairy to glabrous (sometimes with only the marginal hairs). (13) Ligule 0.6 to 1.4 mm long (average 0.8). (14) Leaf blades 4 to 21 cm long (average 14.0);

(15) 2 to 5.2 mm wide (average 4.2); (16) flat; (17) surface antorsely scabrous; (18) adaxially pilose to glabrous; (19) abaxially glabrous (rarely pilose); (20) apices hair-like; (21) margins antorsely serrulate. (22) Inflorescence 2 to 10.8 cm long (average 5.0); (23) densely to loosely contracted; (24) elliptic to ovate; (25) axillary inflorescence absent. (27) Spikelets about the same length throughout the panicle; (28) 2.5 to 10.8 mm long (average 6.8); (29) ovate to lanceolate; (30) 5-flowered; (31) with 1 fertile floret; (32) sterile florets not crowded distally; (33) sterile florets not reflexed. (34) Glumes subequal; (35) pilose; (36) coriaceous; (37) green (straw-coloured on maturing); (38) margins pale green to purplish; (39) apices erose; (40) not concealed by overlapping awns (41) Lower glume 2.4 to 6.6 mm long (average 4.4); (42) 5 to 13-nerved (frequently 8-10); (43) truncate to acute; (44) lanceolate to ovate. (45) Upper glume 2.8 to 8.2 mm long (average 5.2); (46) 5 to 11-nerved (frequently 7-9); (47) truncate to acuminate (rarely mucronate); (48) elliptic. (49) Body of the lowest lemma 1.6 to 4 mm long (average 3.1); (50) 1.8 to 3.5 mm wide (average 2.7); (51) apex obtuse; (52) 9- or rarely 11-nerved; (53) lacking extra nerves between main ones; (54) 1 nerve entering each peripheral awn (two if 11-nerved); (56) surface ribbed on the upper part; (57) smooth; (58) yellow; (60) dorsally convex; (61) hairy on the lower part; (62) hairs as long as, to hairs shorter than, the body; (63) margins ciliate; (64) lacking marginal hyaline lobes. (65) Body width to the length 0.7 to 1.3 (average 1.0). (66) Body length to the length of the awns 0.4 to 1.3 (average 0.6). (67) Awns 9; (68) 1.8 to 7.4 mm long (average 4.4); (69) subequal; (70) bases lacking a thickened ridge; (71) purplish-pink; (72) inner rim of cilia present. (73) Palea of the lowest floret 1.8 to 3.8 mm

long (average 2.7); (74) hairy between the nerves; (75) apex cleft; (76) apex glabrous; (77) hairy on the flaps. (78) Rachilla between lower two florets without a hair tuft. (79) Lemma of the second floret not ribbed; (80) glabrous. (81) Anthers 0.5 to 2 mm long (average 1.1); (82) yellow. (83) Caryopsis 1.1 to 2.1 mm long (average 1.9); (84) 0.8 to 1.8 mm wide (average 1.4); (85) globoid to ellipsoid. (86) Embryo 0.7 to 0.9 the caryopsis length (average 0.8); (87) 0.9 to 1.8 mm long (average 1.4).

Remarks: The species has been confused since the last revision. Burbidge (1941) included under this species material belonging to *E. pallidus*. The species was included in *P. nigricans* by Bentham, Fl. Austral., 7: 600 (1878). The type specimen Brown 6250 was erroneously cited as 5250 by Domin (1915).

Affinities: The species is closely related to *E. decipiens* and *E. eremophilus*. It differs from *E. decipiens* in having one fertile floret per spikelet and a glabrous second lemma; and from *E. eremophilus* in having the leaf blades with hair-like apices, awn bases with an inner rim of cilia, and a palea hairy between the nerves and on the flaps.

Distribution: Northern Territory, Queensland and Western Australia. (Map 3b)

Ecology: The species occurs mainly in tropical and sub-tropical woodlands, arid and semi-arid low woodlands, arid tussock and hummock grasslands, and rarely in Acacia shrublands (Moore 1970). Associated species include *Eucalyptus terminalis*, *E. tectifera*, *E. clavigera*, *E. papuana*, *E. foelscheana*, *E. brevifolia*, *Terminalia canescens*, *Xerochloa laniflora*, annual *Sorghum*, *Triodia intermedia*, *Triodia* spp.,

Iseilema vaginiflorum, *Dichanthium tenuicolum*, *Heteropogon contortus*, *Eragrostis tenellula*, and *Cenchrus ciliaris*. It is common on river flats, river and creek banks, terraced denudated areas, coastal plains, sandy hills, and sometimes pioneering denuded areas and crater floors. The soils range from shallow eroded types to coarse textured skeletal soils, and include red sands, sandy silt clays on clay pans and flats, dark to pale grey loams, desert calcareous, limestone outcrops, basaltic hills, razor sharp volcanic and limestone rocks, and tertiary non-lateritic soils. The grass is regarded as good fodder but it is short lived.

Representative specimens (41/120)

NORTHERN TERRITORY: 31.5 miles N. N. E of Mount Stanford outstation, Perry 2173 (AD BRI CANB); 21 miles S. W of Katherine township, Lazarides 1993 (CANB); 40 miles S. W of Katherine township, Perry 1995 (BRI CANB); Darwin Road, 5 miles N. of Katherine township, Lazarides 2775 (BRI CANB); Rabbit Flat, Latz 3952 (BRI); Elsey creek, Roper River, Byrnes 2581 (BRI CANB); Nicholson River, Henshall 331 (BRI CANB); near Katherine Hospital, Latz 1107 (CANB), Chippendale CANB 160068 (CANB); Mistake creek, Letts NT8377 (CANB); 12 miles N. of Victoria River Downs, Perry 2108 (CANB); 45 km S. W of Mongrel Downs Homestead, Latz 720 (CANB); Victoria River Station, Ganley CANB 144149 (CANB); 37.7 miles S. W of Top Springs Store, Chippendale CANB 218569, 216570 (CANB); S. of Minets Camp, Rice 2210 (CANB); near Wavehill Police Station, Lazarides 6280 (CANB); 28 miles N. of Springvale station, Lazarides 6370 (CANB); 90 miles W. of Granites, Mahood CANB 111751 (CANB); Alroy Downs station, Latz 1549 (CANB); 4 miles N. of Newy, Chippendale CANB 218584 (CANB); Low level bridge at Katherine, Wilson 17 (CANB); S. of Mongrel Downs, Latz 6531 (CANB); McArthur

River, E. of Minets Camp, Craven 3468 (CANB); Victoria River, Mueller s.n, December 1855 (MEL).

QUEENSLAND: Chillagoe, Blake 13512 (BRI).

WESTERN AUSTRALIA: 11 km S. W of Lamboo station, Lazarides 6307 (AD BRI CANB); 1.5 miles W. of Mount House station, Lazarides 6445 (BRI CANB), 5165 (CANB); S. E of Gordon Downs, Perry 2484 (AD BRI CANB); 28 miles N. of Springvale station, Lazarides 6370 (CANB); 10 miles N. of Rockhole station, Lazarides 6362 (CANB); 12 miles W. of Tablelands station, Lazarides 6416 (CANB); Old Fossil Downs road near Fitzroy crossing, Wolfe & Martin 70 (CANB); dry plains of Ord River, 25 km S. E of Wyndham, Paijmans 2486 (CANB); Fossil Diamond Gorge road, 1 km N. E of Fossil Downs Homestead, Beauglehole 53982 (CANB); Karunjie station, Rust LRRS43 (CANB); in the vicinity of Kimberley Reseach station near Kununurra, Mackenzie 690416G-4 (CANB); Ord River, 33 km E. S. E of Wyndham, Paijmans 2512 (CANB); Ord River station, Hooper 10762 (CANB); 10 km N. of Ord River station, Aplin 5419 (PERTH); Ord River, 30 km N. W of Kununurra, Paijmans 2248 (CANB); no specific locality, Connor 12 (PERTH).

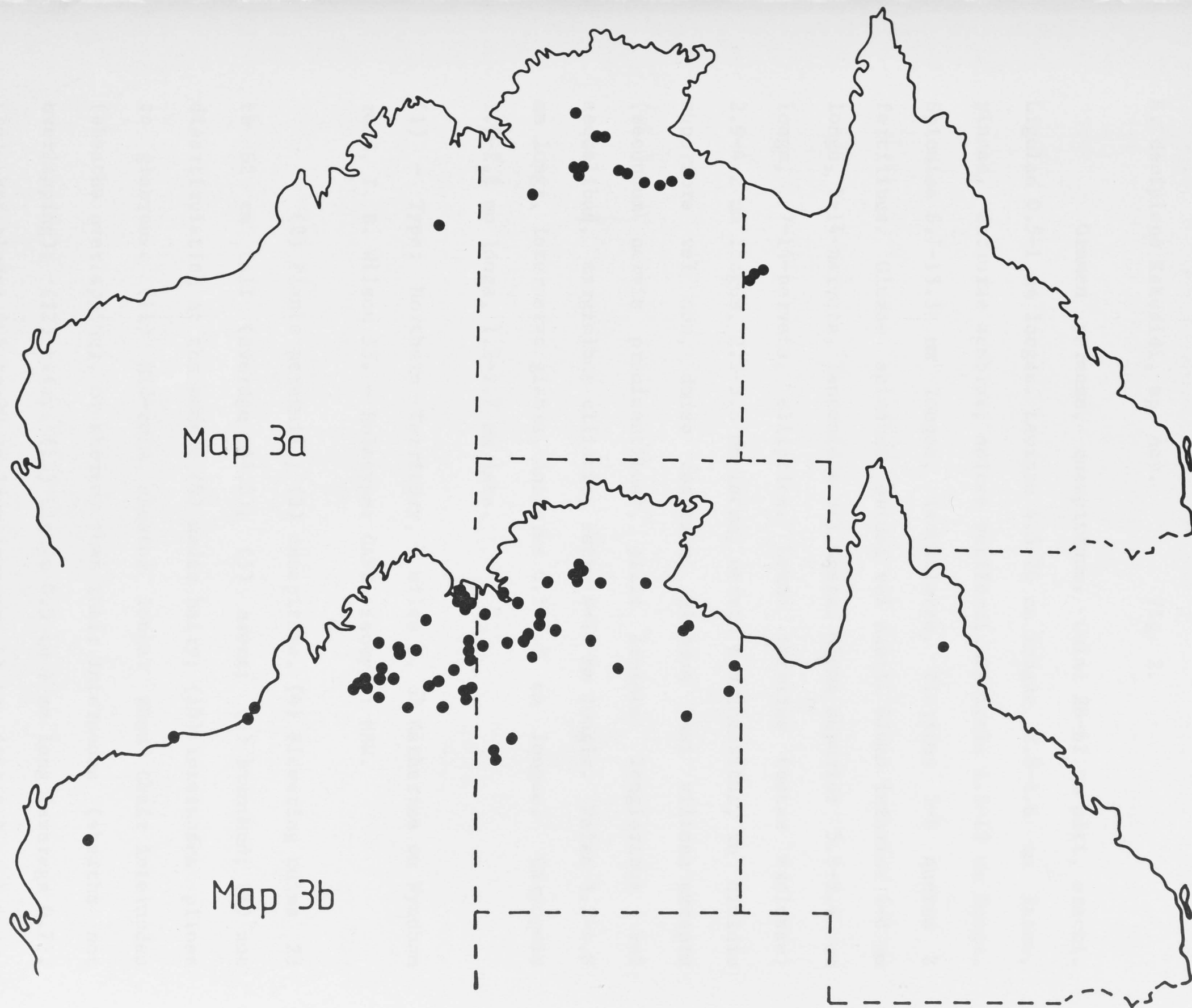
References: Burbidge (1941: 69, with *E. polyphyllus*); Gardner (1952: 30 as *E. glaber* and *E. planifolius*); Cameron (1979, fig. 55); Jessop (1981: 453, as *E. glaber* and *E. planifolius*); Lazarides (1970: 122, pl. 34b as *E. glaber*).

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Map 3a. Distribution of *E. decipiens*.

Map 3b. Distribution of *E. purpurascens*.



5.8.6. *E. decipiens*

E. decipiens Kakudidi, sp. nov.

Fig. 2.

Gramen perenne, caespitosum. Culmi 28-62 cm alti, erecti. Ligulae 0.5-1 mm longae. Laminae 4.5-20 cm longae, 2.8-4.6 mm latae, planae, antrorse scabrae; apices setiformi. Panicula 1.5-13 cm longa. Spiculae 6.7-13.3 mm longae, lanceolatae, floribus 5-6 quorum 2 fertilibus. Glumae apicibus obtusi vel acuti. Gluma inferior 4-8 mm longa, 9-14-nervata, lanceolata vel ovata. Gluma superior 5.9-9.4 mm longa, 7-14-nervata, elliptica. Lemma inferius (setae exclusae) 2.9-4.2 mm longum, 2.3-3.8 mm latum, nervis prominentibus, in dimidio superiore vel non, dorso convexum, glabrum basi villosa excepta (secundum nervis prominentibus), pilis lemmate longioribus vel aequalibus, marginibus ciliatis, setis 4-14 mm longis. Palea 3.3-4.8 mm longa, internervo glabra. Antherae 0.5-2.3 mm longae. Caryopsis 1.9-2.2 mm longa, 1.2-1.7 mm lata.

(1) - Type: Northern Territory, 4 miles S. of Katherine on Wyndham road, I. B. Wilson 53. - Holotype: CANB; isotype: NSW.

(2) Plants perennial; (3) caespitose. (4) Flowering culms 28 to 62 cm tall (average 44.5); (5) erect; (6) branched; (8) not disarticulating at the nodes; (9) nodes hairy; (10) internodes pilose to glabrous. (11) Mid-culm sheaths longer than their internodes (sheaths overlapping), or shorter than their internodes (sheaths not overlapping); (12) hairy. (13) Ligule 0.5 to 1 mm long (average 0.7). (14) Leaf blades 4.5 to 20 cm long (average 11.4); (15) 2.8 to 4.6 mm wide (average 3.6); (16) flat; (17) surface antrorsely scabrous; (18)

adaxially pilose; (19) abaxially pilose; (20) apices hair-like; (21) margins antorsely serrulate. (22) Inflorescence 1.5 to 13 cm long (average 6.0); (23) loosely contracted; (24) elliptic to lanceolate; (25) axillary inflorescence absent. (27) Spikelets about the same length throughout the panicle; (28) 6.7 to 13.3 mm long (average 10.3); (29) lanceolate; (30) 5 to 6-flowered; (31) with 2 fertile florets; (32) sterile florets not crowded distally; (33) sterile florets not reflexed. (34) Glumes subequal; (35) pilose; (36) coriaceous; (37) green (straw-coloured on maturing); (38) margins pale green to purplish; (39) apices erose, or not erose; (40) not concealed by overlapping awns. (41) Lower glume 4 to 8 mm long (average 6.4); (42) 9 to 14-nerved (frequently 9-11); (43) obtuse to acute; (44) lanceolate to ovate. (45) Upper glume 5.9 to 9.4 mm long (average 7.3); (46) 7 to 14-nerved (frequently 9-11); (47) obtuse to acute; (48) elliptic. (49) Body of the lowest lemma 2.9 to 4.2 mm long (average 3.6); (50) 2.3 to 3.8 mm wide (average 3.3); (51) apex obtuse; (52) 9 to 11-nerved; (53) lacking extra nerves between main ones; (54) 1 to 2 nerve(s) entering each peripheral awn; (56) surface ribbed on the upper part, or not ribbed; (57) smooth; (58) yellow; (60) dorsally convex; (61) hairy on the lower part; (62) hairs as long as, to hairs shorter than, the body; (63) margins ciliate; (64) lacking marginal hyaline lobes. (65) Body width to the length 0.8 to 1 (average 0.9). (66) Body length to the length of the awns 0.4 to 0.9 (average 0.7). (67) Awns 9; (68) 4 to 14 mm long (average 6.0); (69) subequal; (70) bases lacking a thickened ridge; (71) purplish-pink; (72) inner rim of cilia present. (73) Palea of the lowest floret 3.3 to 4.8 mm long (average 4.1); (74) glabrous between the nerves (occasionally with sparse hairs on the lower one-half); (75) apex

cleft; (76) apex glabrous; (77) hairy, or rarely glabrous, on the flaps. (78) Rachilla between lower two florets without a hair tuft. (79) Lemma of the second floret not ribbed; (80) hairy on the lower part. (81) Anthers 0.5 to 2.3 mm long (average 1.2); (82) yellow. (83) Caryopsis 1.9 to 2.2 mm long (average 2.0); (84) 1.2 to 1.7 mm wide (average 1.5); (85) obovoid. (86) Embryo 0.75 to 0.9 the caryopsis length (average 0.8); (87) 1.3 to 1.8 mm long (average 1.5).

Affinities: This species is close to *E. eremophilus* but it differs in having two fertile florets per spikelet, awn bases with an inner rim of cilia, a hairy second lemma and a palea with hairy, or rarely glabrous, flaps.

Distribution: Northern Western Australia, Northern Territory and Queensland. (Map 3a)

Ecology: It occurs in arid and semi-arid low woodlands and arid tussock and hummock grasslands (Moore 1970), Eucalyptus forests, *E. pruinosa* parklands and in dry sclerophyll forests and shrublands.

Representative specimens (16/22)

NORTHERN TERRITORY: Darwin and Gulf District, Stuart Highway near Daly Waters, Verdon 822 (AD); 34 miles E. of Stuart Highway, on Borroloola road, Latz 1368 (BRI CANB); 24 miles N. of Newcastle creek, Chippendale 1841 (AD); 25 miles E. of Stuart Highway at Daly Waters, Symon 5090 (CANB); 4 miles S. of Katherine off Wyndham road, Wilson 53 (CANB); Stuart Highway, 35 miles N. of Newcastle Waters, Must 409 (CANB); Limbunya, Dunlop 3508 (CANB); 56 miles E. of Daly Waters, Byrnes 2558 (BRI); outstation, 16°38' S 135°08' E, Blake 17728 (BRI); Elsey Creek, Passlow 147 (BRI); Wallock Ponds, Passlow 124 (BRI); 80

km E. of Daly Waters, Passlow 85 (BRI); near Nutwood Downs Homestead, Blake 17587 (BRI).

QUEENSLAND: 66 km N. E of Camooweal on road to Thornton, Kratzing & Ollerenshaw 1308 (BRI).

WESTERN AUSTRALIA: Old Halls Creek, Wolfe & Martin 57 (CANB); no specific locality, Stephens s.n 1898 (PERTH).

5.8.7. *E. pallidus*

E. pallidus (R. Br.) P. Beauv.

(1) *E. pallidus* (R. Br.) P. Beauv., Ess. Agrostogr., 82 & 162 (1812); Desv., J. Bot., 1: 70 (1815). - *Pappophorum pallidum* R. Br., Prod., 85 (1810). - *P. nigricans* var. *pallidum* (R. Br.) Domin, Biblioth. Bot., 20: 381 (1915). - Type: Northern Territory, Carpentaria, R. Brown 6251. - Holotype: BM, n.v; isotype: K !.

- *P. nigricans* var. *pubiculme* Domin, Biblioth. Bot., 20: 382 (1915).

- Type: Queensland, Chillagoe, collected in February 1910, Domin s.n.

- Holotype: PR, n.v; isotype: K !.

(2) Plants perennial; (3) caespitose. (4) Flowering culms 35 to 88 cm tall (average 67.9); (5) erect; (6) branched; (8) not disarticulating at the nodes; (9) nodes hairy; (10) internodes villous. (11) Mid-culm sheaths longer than their internodes (sheaths overlapping), or shorter than their internodes (sheaths not overlapping); (12) hairy. (13) Ligule 0.4 to 1.2 mm long (average

0.9). (14) Leaf blades 7.5 to 17.5 cm long (average 13.9); (15) 3.2 to 6.6 mm wide (average 4.6); (16) flat; (17) surface antrorsely scabrous; (18) adaxially pilose; (19) abaxially pilose; (20) apices not hair-like; (21) margins antrorsely serrulate. (22) Inflorescence 3.1 to 11.5 cm long (average 6.2); (23) loosely contracted; (24) elliptic to lanceolate; (25) axillary inflorescence absent. (27) Spikelets about the same length throughout the panicle; (28) 5.6 to 12.6 mm long (average 8.6); (29) lanceolate; (30) 4 to 5-flowered; (31) with 1 fertile floret; (32) sterile florets not crowded distally; (33) sterile florets not reflexed. (34) Glumes subequal; (35) pilose; (36) coriaceous; (37) green (straw-coloured on maturing); (38) margins pale green; (39) apices erose; (40) not concealed by overlapping awns. (41) Lower glume 3 to 5.8 mm long (average 4.4); (42) 6 to 11-nerved (frequently 6-9); (43) truncate to obtuse, or mucronate; (44) lanceolate to ovate. (45) Upper glume 3.5 to 6.3 mm long (average 4.7); (46) 5 to 8-nerved; (47) truncate to obtuse, or mucronate; (48) elliptic. (49) Body of the lowest lemma 2 to 3.4 mm long (average 3.1); (50) 2 to 3.2 mm wide (average 2.2); (51) apex obtuse; (52) 9-nerved (rarely 11-nerved); (53) lacking extra nerves between main ones; (54) 1 nerve entering each peripheral awn; (56) surface ribbed on the upper part; (57) papillose; (58) yellow; (60) dorsally convex; (61) hairy on the lower part; (62) hairs as long as the body; (63) margins ciliate; (64) normally lacking marginal hyaline lobes. (65) Body width to the length 0.7 to 1 (average 0.9). (66) Body length to the length of the awns 0.3 to 0.8 (average 0.5). (67) Awns 9; (68) 3 to 9.5 mm long (average 5.5); (69) subequal; (70) bases lacking a thickened ridge; (71) yellow; (72) inner rim of cilia present. (73) Palea of the lowest floret 2.1 to 3.8 mm long (average 3.0); (74)

hairy between the nerves; (75) apex cleft; (76) apex hairy; (77) hairy on the flaps. (78) Rachilla between lower two florets without a hair tuft. (79) Lemma of the second floret not ribbed; (80) glabrous. (81) Anthers 1.1 to 1.4 mm long (average 1.2); (82) yellow. (83) Caryopsis 1.3 to 2 mm long (average 1.8); (84) 0.8 to 1.3 mm wide (average 1.0); (85) obovoid to ellipsoid. (86) Embryo 0.7 to 0.9 the caryopsis length (average 0.8); (87) 0.9 to 1.6 mm long (average 1.4).

Distribution: The species is confined to northern Australia extending through Western Australia, Northern Territory and Queensland. (Map 4)

Ecology: The species occurs in tropical and sub-tropical woodlands, and coastal grasslands (Moore 1970), and low forests of Bauhinia, Terminalia and Melaleuca spp. Soils range from sands on stabilized coastal dunes to saline loams, limestone, and calcareous dunes.

Representative specimens (27/61)

NORTHERN TERRITORY: Wessel Islands, Latz 3248 (BRI CANB); Bing Bong station, Latz 1475 (CANB); Warangaye Lagoon, Elcho Island, Latz 6051 (CANB); Carambirini waterhole, Latz 2172 (CANB); 8 km S. E of Larrimah, Winkworth 1092 (CANB); Barkly Tablelands, Nicholson River area, Fish River crossing, Kanis 1972 (CANB); Central District, Pullen 6898 (CANB); 21 miles S. of Elliot, Stuart Highway, Must 370 (CANB); Groote Eylandt, Emenbungwa, S of Dalumbu Bay, Wanddy 779 (CANB); Gulf of Carpentaria, Maria Island, Dunlop 2786 (CANB); 48 km E. of Daly Waters, Passlow 89 (BRI); 40 km E. of Daly Waters, Passlow 2563 (BRI); Port Bradshaw, Specht 712 (AD BRI); South Bay, Bickerton Island, Specht 653 (AD BRI); Hampe Bay, Groote Eylandt, Specht 280 (AD BRI); Black Point, Byrnes & Maconochie 1055 (AD); 13 miles S. of Katherine, Wilson 145 (BRI).

QUEENSLAND: Chillagoe, Hubbard & Winders 6782 (BRI CANB); Edward River Mission, Pedley 2688 (BRI); Gilbert River, White 1494 (BRI); Domadgee Mission near Burketown, Whitehouse BRI 286812 (BRI); 28 km S. S. E of Normanton, Beeston 32 (BRI); Adel's Grove, de Lestang 308 (BRI); 25 km S. S. E of Normanton, Beeston 10 (BRI); 5 km W. of Domadgee, Jacobs 1444 (CANB).

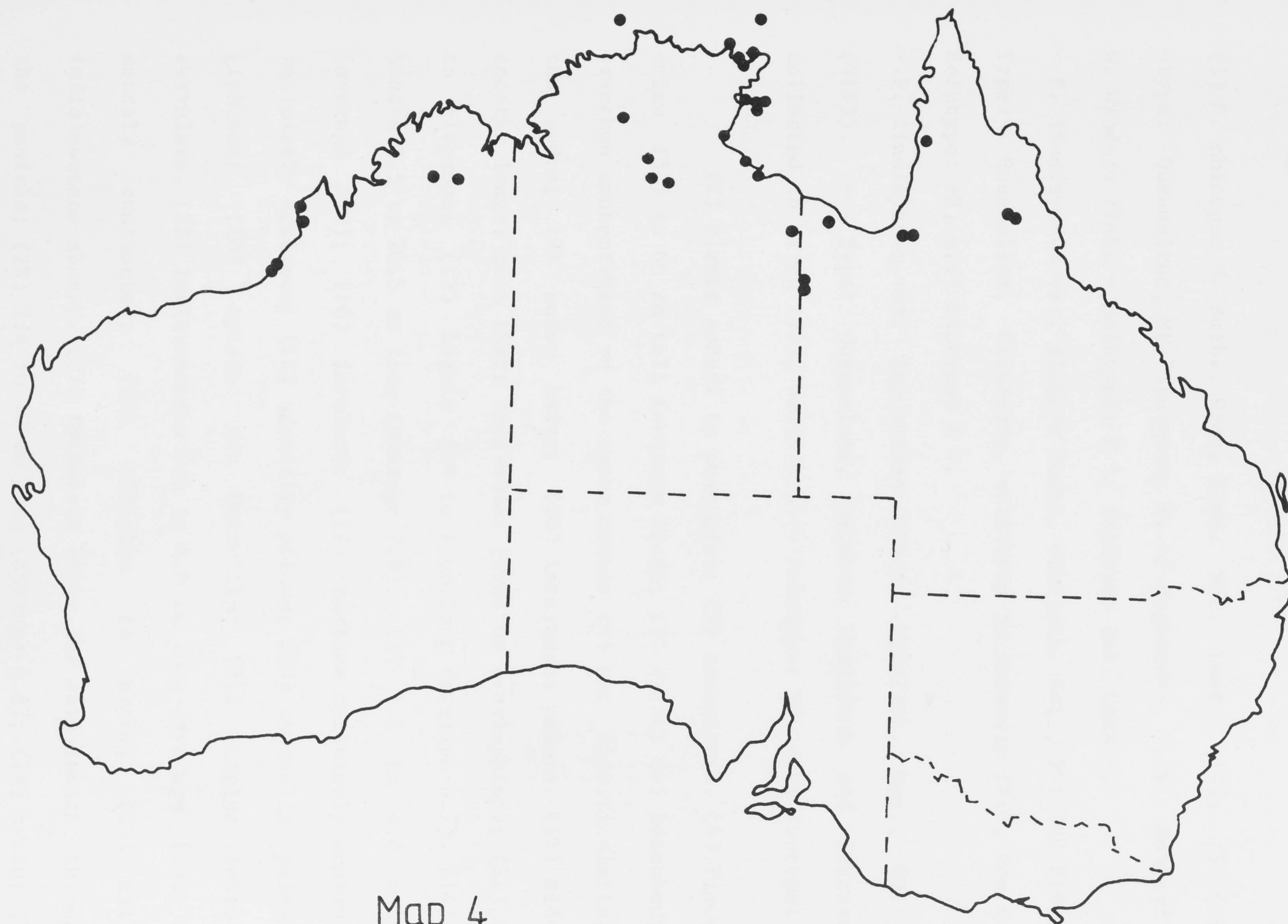
WESTERN AUSTRALIA: Broome, Gardner 7016 (BRI); Karunjie station, Kimberleys, Rust LRRS29 (CANB).

NEW GUINEA: Leron, Morobe district, Henty 180 (CANB).

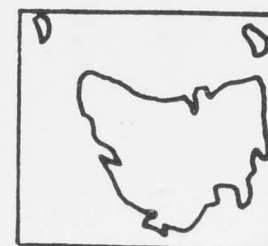
References: Burbidge (1941: 79, with *E. conicus*); Cameron (1979: 180, with *E. conicus*).

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Map 4. Distribution of *E. pallidus*.



Map 4



5.8.8. *E. oblongus*

E. oblongus N. Burb.

(1) *E. oblongus* N. Burb., Proc. Linn. Soc. Lond., 153: 85 (1941).

-Type: Queensland, Mt. Sturgeon, N. of Hughenden, C. E. Hubbard & C.

W. Winders 7745. - Holotype: K !, isotype: BRI, CANB !.

- *P. lindleyanum* var. *glaucum* Domin, Biblioth. Bot., 20: 380 (1915). -

Type: Queensland, Cloncurry, collected in February 1910, Domin s.n.

Holotype: PR, n.v; isotype: K !.

- *P. lindleyanum* var. *laguroides* Domin, Biblioth. Bot., 20: 380

(9115). - Type: Queensland, between Longreach and Ilfracombe,

collected in March 1910, Domin s.n. - Holotype: PR, n.v; isotype: K !.

(2) Plants annual to perennial; (3) caespitose. (4) Flowering culms 13.5 to 66 cm tall (average 36.8); (5) erect; (6) branched; (7) branches concentrated on the upper nodes; (8) not disarticulating at the nodes; (9) nodes hairy; (10) internodes pilose. (11) Mid-culm sheaths longer than their internodes (sheaths overlapping); (12) hairy to glabrous. (13) Ligule 0.4 to 1 mm long (average 0.7). (14) Leaf blades 1.5 to 20.5 cm long (average 7.8); (15) 1.8 to 4.8 mm wide (average 3.0); (16) involute; (17) surface antrorsely scabrous to retrorsely scabrous; (18) adaxially pilose; (19) abaxially pilose to glabrous; (20) apices not hair-like; (21) margins antrorsely serrulate. (22) Inflorescence 0.6 to 4.6 cm long (average 1.6); (23) densely contracted; (24) elliptic to ovate; (25) axillary inflorescence absent. (27) Spikelets about the same length throughout the panicle; (28) 2.4 to 10 mm long (average 6.8); (29) ovate; (30) 4 to 6-flowered; (31) with 1 fertile floret; (32) sterile florets not

crowded distally; (33) sterile florets not reflexed. (34) Glumes subequal; (35) pilose; (36) membranous; (37) green (straw-coloured on maturing); (38) margins pale green to purplish; (39) apices erose; (40) not concealed by overlapping awns. (41) Lower glume 1.9 to 4.8 mm long (average 3.3); (42) 4 to 12-nerved (frequently 5-9); (43) truncate to obtuse; (44) oblong to elliptic. (45) Upper glume 2.6 to 5 mm long (average 3.8); (46) 3 to 8-nerved (frequently 5-7); (47) truncate to obtuse; (48) oblong to elliptic. (49) Body of the lowest lemma 1.7 to 4.3 mm long (average 2.7); (50) 1.3 to 2.9 mm wide (average 1.7); (51) apex truncate; (52) 9 to 11 -nerved (rarely 12-16); (53) with extra nerves between main ones; (54) 1 to 2 nerve(s) entering each peripheral awn; (55) surface deeply ribbed; (58) yellow to purplish-pink; (59) oblong; (60) dorsally straight; (61) hairy on the lower part; (62) hairs as long as the body; (63) margins ciliate; (64) normally lacking marginal hyaline lobes. (65) Body width to the length 0.5 to 1.2 (average 0.8). (66) Body length to the length of the awns 0.5 to 1.2 (average 0.8). (67) Awns 9 to 12; (68) 1.6 to 6.2 mm long (average 3.1); (69) subequal; (70) bases lacking a thickened ridge; (71) purplish-pink; (72) inner rim of cilia present. (73) Palea of the lowest floret 2.2 to 4.4 mm long (average 3.1); (74) hairy between the nerves; (75) apex truncate; (76) apex glabrous; (77) hairy on the flaps. (78) Rachilla between lower two florets without a hair tuft. (79) Lemma of the second floret not ribbed (rarely ribbed); (80) glabrous. (81) Anthers 0.5 to 2.2 mm long (average 0.9); (82) yellow. (83) Caryopsis 1.1 to 2.2 mm long (average 1.5); (84) 0.7 to 1.1 mm wide (average 0.9); (85) obovoid to ellipsoid. (86) Embryo 0.5 to 0.8 the caryopsis length (average 0.7); (87) 0.8 to 1.5 mm long (average 1.1).

Affinities: The species is closely related to *E. lindleyanus* but it differs mainly by having a deeply ribbed lemma and a palea with a glabrous apex.

Distribution: Northern Territory, Queensland, Western Australia, and South Australia. (Map 5)

Ecology: The species occurs commonly in brigalow forests, tropical and sub-tropical woodlands, semi-arid shrub woodlands, *Acacia* shrublands and arid tussock and hummock grasslands (Moore 1970). Associated species include *Eucalyptus terminalis*, *E. brevifolia*, *E. papuana*, *Acacia aneura*, *A. nana*, *A. cambagei*, *A. harpophylla*, *Bursaria incana*, *Triodia molesta*, *T. longiceps*, *T. roscida*, *T. stenostachya*, *T. basedowii*, *Sporobolus* sp., *Enteropogon* sp., *Enneapogon* spp., *Digitaria* sp. Soils range from skeletal rocky types on granite, quartzite and limestone outcrops to sandy levees on rivers and creeks, reddish brown sands, dark loams to heavy clay loam and fine silt.

Representative specimens (45/213)

NORTHERN TERRITORY: Dry hills N. of Alice Springs, Gauba 644 (GAUBA); Breakaway W. of Toko Ranges, Purdie 2226 (CANB); Ruby Cap, Purdie 2398C (CANB); Mount Doreen station, Latz 2033, 2016 (CANB); 5 miles S. W of Huckitta, Parker 230 (CANB); Mount Napier, Dunlop 4071 (CANB); Ringwood station, Latz 4448 (AD CANB); Standley Chasm, Latz 1022 (CANB), Nelson (CANB); Mount Gillen, Simpson Gap National Park, Nelson 2117 (CANB); Wallogarang Homestead, Calvet Hill road, Jacobs 1574 (CANB); Palm Valley, Latz 398, 5293 (CANB); 24 miles S. S. W of Lucy Creek station, Lazarides 5229 (CANB); Mapata Waterhole, 20 miles N. N. E of Huckitta Homestead, Latz 1098 (CANB); 25 miles N. E of Undoolya station, Perry 3280 (CANB); 35 miles W. of Alice Springs, Glen Helen

road, Latz 1040 (CANB); 47 miles S. W of Montejinni station, Lazarides 2893 (AD CANB), Perry 7893 (CANB); 4.5 miles N. of Alice Springs, Latz 1003 (CANB); Hale River crossing, 100 miles E. S. E. of Alice Springs, Perry 5439 (AD CANB); Standley Chasm, Heavitree Range, Carr 1316 and Beauglehole 45093 (CANB); Serpentine Gorge, Carr 1435 and Beauglehole 45214 (CANB); Finke River, Hermannsburg, Hill 69 (BRI).

QUEENSLAND: 2 miles N. E of Dajarra, Lazarides 4042 (CANB); Duchess, Hubbard 7366 (CANB); 7 miles E. of Twin Hills Post Office, Adams 1044 (CANB); Mount Sturgeon station, Hubbard & Winders 7745 (CANB); Mount Isa Township, Lazarides 4366 (CANB); Fairlight station, Hubbard & Winders 7482 (CANB); Jardine Valley near Hughenden, Hubbard & Winders 7182 (CANB); W. of Cloncurry, Beaumont 7058 (CANB); Blackall, Everist BRI 286783 (BRI); Cloncurry, Blake 6376 (BRI); Selwyn, Blake 6407 (BRI).

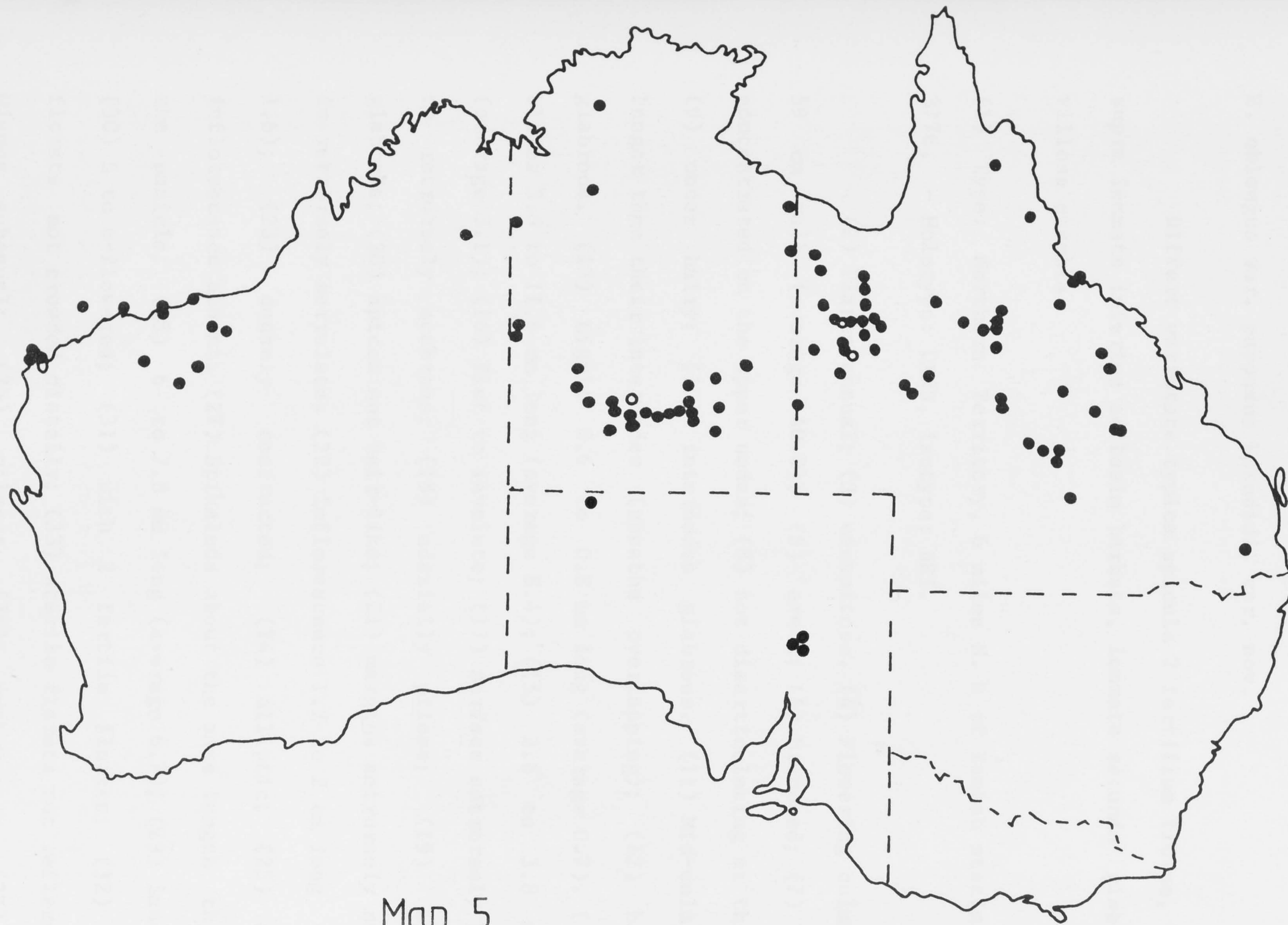
SOUTH AUSTRALIA: foot of Mount Woodroffe, Wilson 2560 (AD); Mount Chambers Gorge, Cleland AD 96244013, AD 96244009 (AD), Williams 332 (AD), Herb. Black AD 97519233-1 & 2 (AD); Mount Chambers, Whibley 5626, 5572 (AD); Balcanoona Homestead, Lothian 3287 (AD); Palalana, Corrick 2014 (AD).

WESTERN AUSTRALIA: Chichester Range, 216 km S. of Port Hedland on the Witenoom road, Pullen 10917 (AD); S. E of Port Hedland, Beauglehole 11354 (PERTH); Slothole Canyon, Cape Range, George 10318 (PERTH); Mundabullangana station, George 3408 (PERTH).

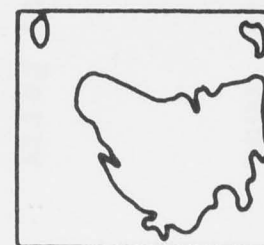
References: Black (1978: 186); Jessop (1981: 455, fig. 580D); Lazarides (1970: 124, pl. 35b; pl. 35a as *E. lindleyanus*).

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Map 5. Distribution of *E. oblongus* (●) and *E. oblongus* var. *papposus* (o).



Map 5



5.8.8.1. Var. papposus

E. oblongus var. *papposus* Kakudidi, var. nov.

Differt varietate typica spicula 2 fertilium florum, rachilla supra lemmate inferius ad basim barbata, lemmate secunda glabra basi villosa excepta.

(1) Type: Northern Territory, 6 miles N. E of Yambah station, Perry 3776. - Holotype: CANB, isotype: BRI.

(2) Plants annual; (3) caespitose. (4) Flowering culms 26 to 59 cm tall (average 40.0); (5) erect; (6) branched; (7) branches concentrated on the upper nodes; (8) not disarticulating at the nodes; (9) nodes hairy; (10) internodes glabrous. (11) Mid-culm sheaths longer than their internodes (sheaths overlapping); (12) hairy to glabrous. (13) Ligule 0.6 to 0.8 mm long (average 0.7). (14) Leaf blades 5.6 to 11.6 cm long (average 8.4); (15) 2.6 to 3.8 mm wide (average 3.1); (16) flat to involute; (17) surface antrorsely scabrous to retrorsely scabrous; (18) adaxially pilose; (19) abaxially glabrous; (20) apices not hair-like; (21) margins antrorsely serrulate to retrorsely serrulate. (22) Inflorescence 1.2 to 2 cm long (average 1.6); (23) densely contracted; (24) elliptic; (25) axillary inflorescence absent. (27) Spikelets about the same length throughout the panicle; (28) 6 to 7.8 mm long (average 6.7); (29) lanceolate; (30) 5 to 6-flowered; (31) with 2 fertile florets; (32) sterile florets not crowded distally; (33) sterile florets not reflexed. (34) Glumes subequal; (35) pilose; (36) membranous; (37) green (straw-coloured at maturity); (38) margins pale green to purplish;

(39) apices erose; (40) not concealed by overlapping awns. (41) Lower glume 4 to 4.8 mm long (average 4.3); (42) 6 to 9-nerved; (43) truncate to obtuse; (44) oblong. (45) Upper glume 4 to 4.8 mm long (average 4.3); (46) 5 to 7-nerved; (47) truncate to obtuse; (48) oblong. (49) Body of the lowest lemma 2.5 to 3.4 mm long (average 3.1); (50) 2.2 to 2.8 mm wide (average 2.4); (51) apex truncate; (52) 9 to 13-nerved; (53) with extra nerves between main ones; (54) 2 nerves entering each peripheral awn; (55) surface deeply ribbed; (57) smooth; (58) yellow; (59) oblong; (60) dorsally straight; (61) hairy on the lower part; (62) hairs as long as the body; (63) margins ciliate; (64) normally lacking marginal hyaline lobes. (65) Body width to the length 0.7 to 0.9 (average 0.8). (66) Body length to the length of the awns 0.8 to 0.9. (67) Awns 9; (68) 3.2 to 3.9 mm long (average 3.6); (69) subequal; (70) bases lacking a thickened ridge; (71) yellow, or purplish-pink; (72) inner rim of cilia present. (73) Palea of the lowest floret 3 to 3.6 mm long (average 3.4); (74) hairy between the nerves; (75) apex cleft; (76) apex glabrous; (77) hairy on the flaps. (78) Rachilla between lower two florets with a hair tuft. (79) Lemma of the second floret ribbed; (80) hairy on the lower part. (81) Anthers 0.8 mm long; (82) yellow. (83) Caryopsis 1.7 to 1.9 mm long (average 1.8); (84) 1 to 1.2 mm wide (average 1.1); (85) obovoid to ellipsoid. (86) Embryo 0.7 to 0.8 the caryopsis length; (87) 1.1 to 1.5 mm long (average 1.3).

Affinities: The variety differs from the typical one by having a tuft of hairs on the rachilla between the lower two florets and the second lemma hairy and ribbed.

Distribution: Northern Territory and Queensland. (Map 5)

Ecology: Associated species include *Eucalyptus terminalis* and *Triodia longiceps*, and *Acacia aneura* on skeletal soils on limestone, rocky sandstone and quartzite.

Representative specimens (3/5)

NORTHERN TERRITORY: 6 miles N. E of Yambah station, Perry 3376 (BRI CANB);

QUEENSLAND: Mount Isa, McCallum s.n (CANB); 29 miles E. of Dajarra township, Lazarides 4564 (CANB).

5.8.9. *E. lindleyanus*

E. lindleyanus (Domin) C. E. Hubb.

(1) *E. lindleyanus* (Domin) C. E. Hubb., Kew Bull., 1934: 450 (1934).

- *Pappophorum lindleyanum* Domin, Biblioth. Bot., 20: 379 (1915). -

Type: Western Australia, Dampier Archipelago, off the N. W coast, Walcot's first specimen (Burbidge 1941), K, n.v.

- *P. lindleyanum* var. *convolutum* Domin, p. 380, loc. cit. - Type: Queensland, Chillagoe, collected in February 1910, Domin s.n. - Syntype: PR, n.v; isosyntype: K !

- *E. pallidus* var. *breviseta* N. Burb., Proc. Linn. Soc. Lond., 153: 81 (1941). - Type: Queensland, Callide, Biloela, Cowdry 23. - Holotype: K, isotype: BRI !.

(2) Plants perennial (short-lived); (3) caespitose. (4) Flowering culms 20 to 45 cm tall (average 29.6); (5) erect; (6) branched; (7) branches concentrated on the upper nodes; (8) not

disarticulating at the nodes; (9) nodes hairy; (10) internodes pilose. (11) Mid-culm sheaths shorter than their internodes (sheaths not overlapping); (12) hairy to glabrous. (13) Ligule 0.5 to 1 mm long (average 0.8). (14) Leaf blades 3.5 to 11.9 cm long (average 6.8); (15) 2 to 4.8 mm wide (average 3.2); (16) involute; (17) surface antrorsely scabrous; (18) adaxially pilose; (19) abaxially glabrous; (20) apices not hair-like; (21) margins antrorsely serrulate. (22) Inflorescence 0.9 to 2.5 cm long (average 1.5); (23) densely contracted; (24) elliptic to ovate; (25) axillary inflorescence absent. (27) Spikelets about the same length throughout the panicle; (28) 4 to 7.2 mm long (average 5.2); (29) ovate; (30) 3 to 5-flowered (frequently 4); (31) with 1 fertile floret; (32) sterile florets not crowded distally; (33) sterile florets not reflexed. (34) Glumes subequal; (35) pilose to glabrous; (36) membranous; (37) green to grey; (38) margins pale green to purplish; (39) apices erose; (40) not concealed by overlapping awns. (41) Lower glume 2 to 3.5 mm long (average 2.8); (42) 4 to 9-nerved (frequently 5.7); (43) truncate to obtuse, or mucronate; (44) oblong to elliptic. (45) Upper glume 2.4 to 4 mm long (average 3.0); (46) 4 to 7-nerved; (47) truncate to obtuse, or mucronate; (48) oblong to elliptic. (49) Body of the lowest lemma 1.8 to 3.2 mm long (average 2.3); (50) 1.4 to 2.2 mm wide (average 1.8); (51) apex truncate; (52) 9-nerved; (53) lacking extra nerves between main ones; (54) 1 nerve entering each peripheral awn; (55) surface shallowly ribbed; (58) yellow; (59) oblong; (60) dorsally convex to straight; (61) hairy on the lower part; (62) hairs as long as the body; (63) margins ciliate; (64) lacking marginal hyaline lobes. (65) Body width to the length 0.5 to 1 (average 0.8). (66) Body length to the length of the awns 0.8 to 1.7 (average 1.1). (67) Awns

9; (68) 1.5 to 4.2 mm long (average 2.4, stiff and plumose in the lower three fourths of their length); (69) subequal; (70) bases lacking a thickened ridge; (71) yellow to purplish-pink; (72) inner rim of cilia present. (73) Palea of the lowest floret 2.1 to 3.6 mm long (average 2.8); (74) hairy between the nerves; (75) apex cleft; (76) apex hairy; (77) hairy on the flaps. (78) Rachilla between lower two florets without a hair tuft. (79) Lemma of the second floret not ribbed; (80) glabrous. (81) Anthers 0.6 to 1.6 mm long (average 1.0); (82) yellow. (83) Caryopsis 1.3 to 2 mm long (average 1.6); (84) 0.7 to 1 mm wide (average 0.9); (85) ellipsoid. (86) Embryo 0.5 to 0.9 the caryopsis length (average 0.7); (87) 0.9 to 1.4 mm long (average 1.1).

Remarks: Burbidge (1941) examined two specimens of Walcot's labelled *Pappophorum lindleyanum*, Dampier Archipelago. One agreed with var. *convolutum* and was retained as the type of *E. lindleyanus* while the other, a more robust specimen, was included in *E. oblongus*. Other Domin specimens of *P. lindleyanum* var. *convolutum* were from Castle Hill near Townsville, and Chillagoe in Queensland. *E. pallidus* var. *breviseta* N. Burb. was found to be similar to *E. lindleyanus* and has been sunk into synonymy.

Affinities: The species is closely related to *E. oblongus*, but it differs by having a shallowly ribbed lemma, a palea with a hairy apex, and stiff awns that are plumose in the lower three-fourths of their length.

Distribution: Northern Territory and Queensland. (Map 6a)

Ecology: The species occurs mainly in tropical and sub-tropical woodlands, brigalow forests, and semi-arid shrublands (Moore 1970).

Associated species include *Eucalyptus thozetiana*, *E. melanophloia*, *E. drepanophylla*, *E. maculata*, *Acacia coriacea*, *A. catenulata*, *Callitris columellaris* and *Chenopodium pseudomicrophylla*. Soils range from skeletal rocky types on hill slopes to sands and limestone outcrops.

Representative specimens (30/49)

NORTHERN TERRITORY: 115 km E. of Stuart Highway on Borroloola road, Dunlop 2157 (CANB); 0.5 miles N. of Tennant Creek township, Perry 528 (CANB); Yaya Creek, Cleland AD 97215016 (AD).

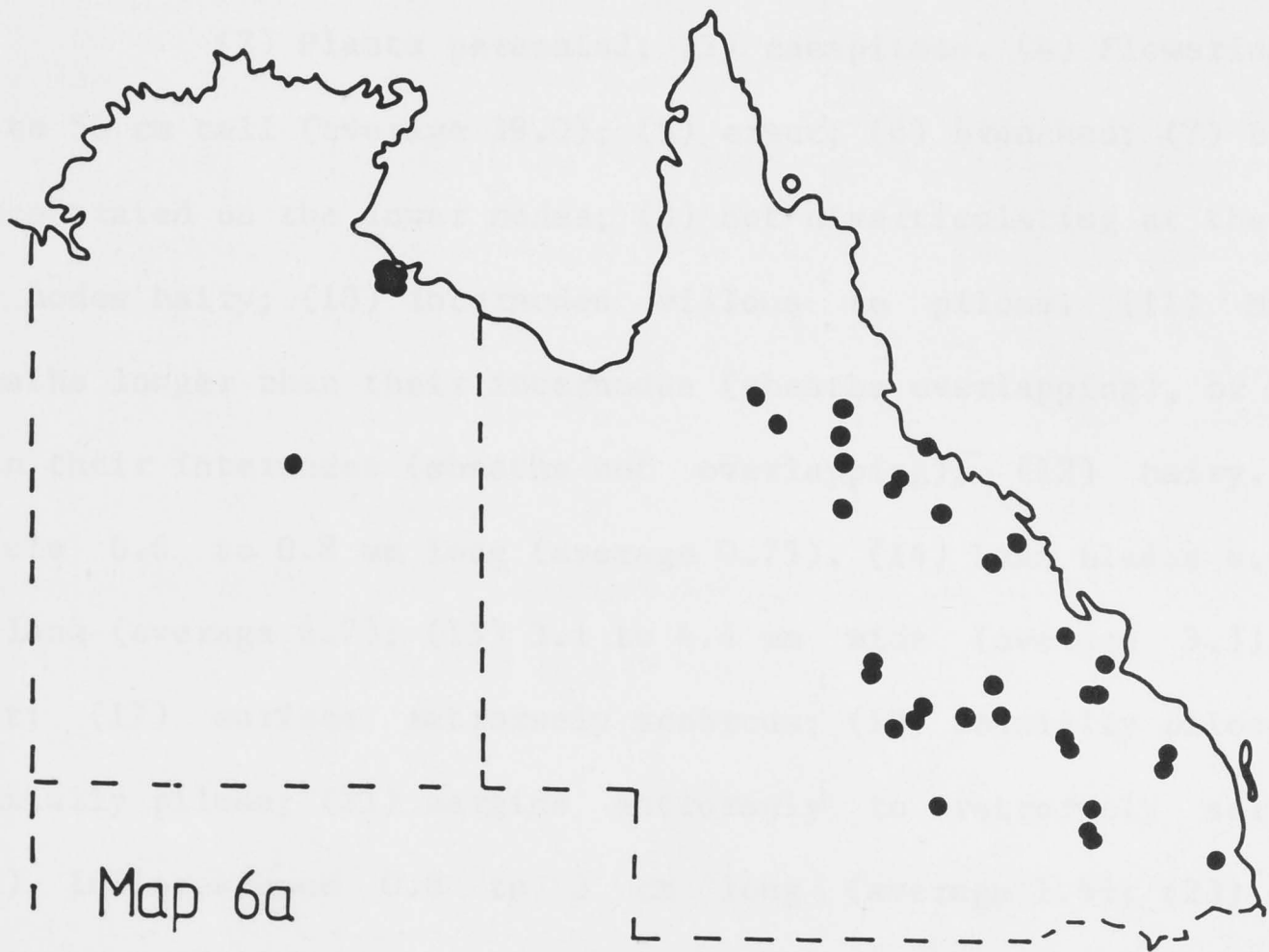
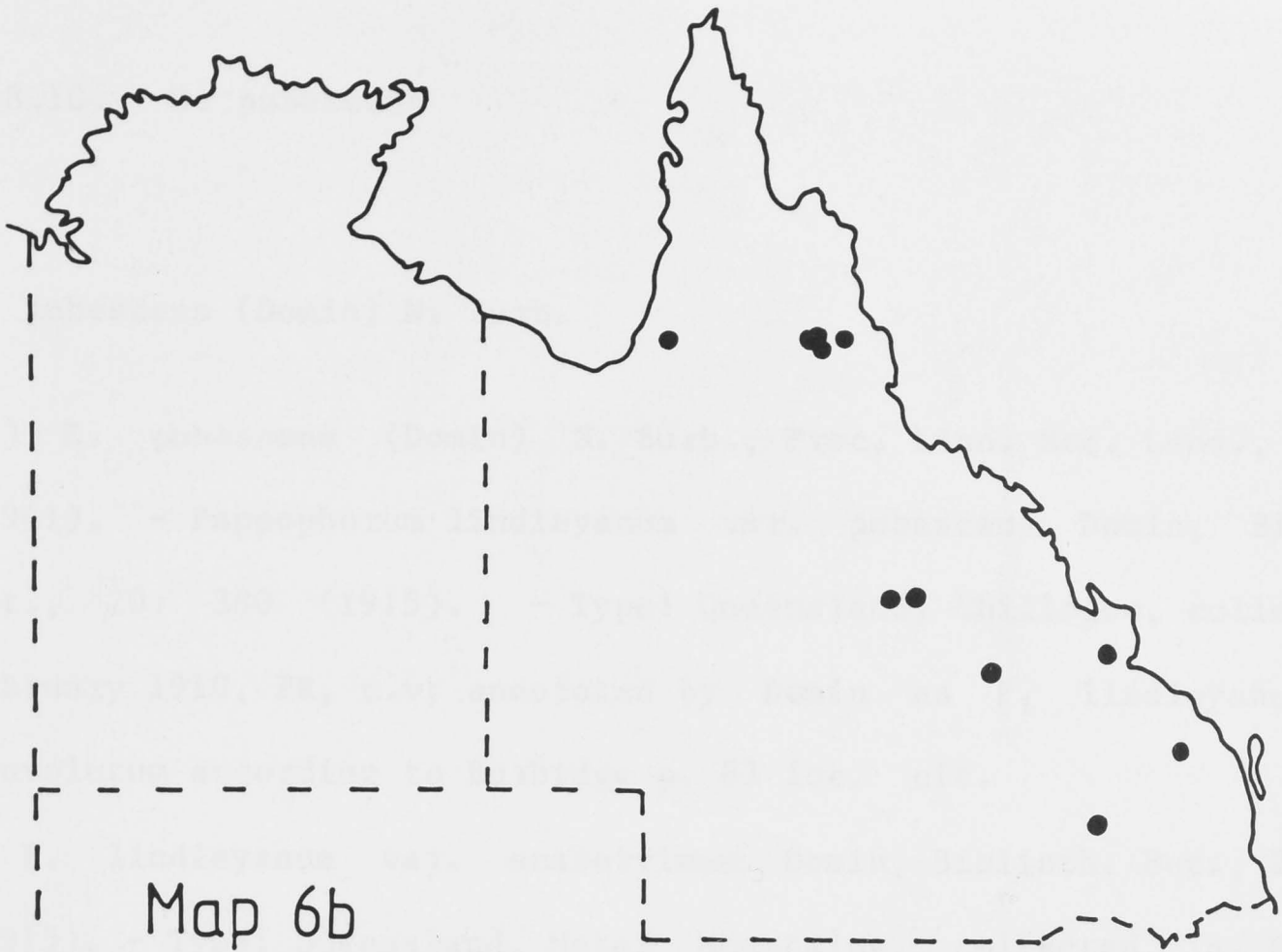
QUEENSLAND: Lake Elphinstone, Anderson 253 (BRI); Broadsound Range, Simon & Andrew 2568 (BRI CANB); Minerva, Blake 7026 (BRI); Isla Gorge, Sharp & Hockings 562 (BRI); 3 miles N. of Tanderra station, Adams 1382 (CANB); 40 km S. E of Jericho, Beeston 1293C (BRI); 37 km W. of Jericho - Barcaldine road, Beeston 1248 (BRI); 15 km N. W of Tambo, Beeston 134C (BRI); 55 km N. N. E of Tambo, Beeston 1325C (BRI); Griffith siding, 4 km E. of Mungana, Conn & De Compo 1320 (CANB MEL); Flinders Island, Clarkson 2292 (BRI CANB); Chillagoe, Hubbard & Winders 6763 (BRI); Cumberland, Gilbert River, Brass 8796 (BRI CANB); 90 km N. N. W of Chinchilla, Lithgow 525 (BRI); Mount Blandy, Forster 515 (BRI); near Gurulmundi, Hubbard 5172 (BRI); Dogwood creek, E. of Gurulmundi, Belson 1930 (BRI); Castle Hill, Townsville, Hubbard & Winders 6630 (BRI CANB); near Pentland, Blake 6138 (BRI); N. W of Charters Towers, Maryvale, Blake 19413 (BRI); Christmas Creek station, Thorsborne 71 (BRI); between Hunt and Oak Hill, 60 miles S. of Mount Garnet, Moraine 132 (BRI); 63 km N. E of Tambo, Beeston 1186C (BRI); Hazlewood creek, on road to Augathella Dam, Simon 3340 (BRI); Lake Manchester, 35 km W. of Brisbane, Sharp 2352 (BRI); Victoria Downs, 5 miles N. W OF Morven, Everist 3765 (BRI);

NEW GUINEA: Lea Lea, W. of Port Moresby, Pullen 3810 (CANB).

References: Black (1978: 186); Burbidge (1941: 82); Cameron (1979: 172); Gardner (1952: 32); Jessop (1981: 454).

Map 6b. Distribution of *E. pubescens*.

Map 6a. Distribution of *E. lindleyanus*.



5.8.10. *E. pubescens*

E. pubescens (Domin) N. Burb.

(1) *E. pubescens* (Domin) N. Burb., Proc. Linn. Soc. Lond., 153: 83 (1941). - *Pappophorum lindleyanum* var. *pubescens* Domin, Biblioth. Bot., 20: 380 (1915). - Type: Queensland, Chillagoe, collected in February 1910, PR, n.v; annotated by Domin as *P. lindleyanum* var. *convolutum* according to Burbidge p. 83 loc. cit.

- *P. lindleyanum* var. *scaberrimum* Domin, Biblioth. Bot., 20: 383 (1915). - Type: Queensland, Metal Mountains, collected in February 1910, Domin s.n. - Holotype: PR, n.v; isotype: K !.

(2) Plants perennial; (3) caespitose. (4) Flowering culms 24 to 56 cm tall (average 39.0); (5) erect; (6) branched; (7) branches concentrated on the lower nodes; (8) not disarticulating at the nodes; (9) nodes hairy; (10) internodes villous to pilose. (11) Mid-culm sheaths longer than their internodes (sheaths overlapping), or shorter than their internodes (sheaths not overlapping); (12) hairy. (13) Ligule 0.6 to 0.8 mm long (average 0.75). (14) Leaf blades 4.4 to 12 cm long (average 6.7); (15) 3.1 to 4.4 mm wide (average 3.5); (16) flat; (17) surface retrorsely scabrous; (18) adaxially pilose; (19) abaxially pilose; (21) margins antrorsely to retrorsely serrulate. (22) Inflorescence 0.8 to 3 cm long (average 1.9); (23) densely contracted; (24) oblong to elliptic; (25) axillary inflorescence absent. (27) Spikelets about the same length throughout the panicle; (28) 4.2 to 7.6 mm long (average 5.8); (29) lanceolate (to oblong); (30) 4 to 5-flowered; (31) with 1 fertile floret; (32) sterile florets not crowded distally; (33) sterile florets not reflexed. (34) Glumes

subequal; (35) pilose; (36) membranous; (37) green (straw-coloured at maturity); (38) margins pale green; (39) apices erose; (40) not concealed by overlapping awns. (41) Lower glume 2.4 to 3.9 mm long (average 3.2); (42) 5 to 9 -nerved; (43) truncate to obtuse; (44) oblong to elliptic. (45) Upper glume 2.4 to 4.5 mm long (average 3.4); (46) 4 to 6-nerved; (47) truncate to obtuse; (48) elliptic. (49) Body of the lowest lemma 2.2 to 3.2 mm long (average 2.6); (50) 1.4 to 2.4 mm wide (average 2.0); (51) apex truncate; (52) 9-nerved; (53) lacking extra nerves between main ones; (54) 1 nerve entering each peripheral awn; (55) surface deeply ribbed; (58) yellow; (59) oblong; (60) dorsally convex; (61) hairy on the lower part; (62) hairs as long as the body; (63) margins ciliate; (64) normally lacking marginal hyaline lobes. (65) Body width to the length 0.6 to 0.9 (average 0.7). (66) Body length to the length of the awns 0.7 to 1 (average 0.9). (67) Awns 9; (68) 2.2 to 4.6 mm long (average 3.1); (69) subequal; (70) bases lacking a thickened ridge; (71) yellow; (72) inner rim of cilia present. (73) Palea of the lowest floret 2.4 to 3.6 mm long (average 2.7); (74) hairy between the nerves; (75) apex cleft; (76) apex hairy; (77) hairy on the flaps. (78) Rachilla between lower two florets without a hair tuft. (79) Lemma of the second floret not ribbed; (80) glabrous. (81) Anthers 1.1 to 1.6 mm long (average 1.3); (82) yellow.

Remarks: Domin distinguished *Pappophorum lindleyanum* var. *convolutum* from var. *pubescens* by the latter possessing pubescent leaves. Burbidge (1941) having not seen any specimens of var. *pubescens*, chose one labelled var. *convolutum* as the type for *E. pubescens*, although not included in the list of localities given by Domin.

Affinities: The species is closely related to *E. lindleyanus* but it

differs by having retrorsely scabrous leaves and being branched from the lower nodes.

Distribution: Queensland. (Map 6b)

Ecology: The species appears to be restricted to eastern Queensland in tropical and sub-tropical woodlands, brigalow forests, and semi-arid shrublands and woodlands (Moore 1970). Associated species include *Eucalyptus tessellaris*, *E. cullenii*, *E. melanophloia*, *Lysiphyllum cunninghamii*, *Brachychiton australe*, *Lepturus xerophilus*, *Perotis rara*, *Eragrostis cumingii*, *Hackelochloa granularis*, *Arundinella setosa*, *Paspalidium gracile*, *Panicum seminudum*, *Panicum* spp., etc.

Representative specimens (12/14)

QUEENSLAND: Moomera, Cole & Provan 5051 (BRI); 16 km N. W of Jericho near Edwinstowe Homestead, Beeston 1309C (BRI); 9 km S. of Emerald, Bisset s.n, 19 x 1964 (BRI); Epping Forest National Park near Clermont, Wilkinson A30 (BRI); near Mingo Crossing on Burnett River, Foster 1063 (BRI); Chillagoe, Hubbard & Winders, 6763 (BRI CANB); Chillagoe - Almaden road, 8 km from Chillagoe, Simon & Clarkson 3557 (BRI); Almaden - Petford road, 4 km from Almaden, Simon & Clarkson 3602 (BRI); Dogwood creek, E. of Gurulmundi, Belson s.n 1930 (BRI); Gilbert River, White 1493 (BRI); Forest Home Station, Brass 1855 (BRI); between Boonmoo and Dimbulah, Hubbard & Winders 6859 (BRI).

Reference: Burbidge (1941: 83, fig. 4).

5.8.11. *E. asperatus*

E. asperatus C. E. Hubb.

(1) *E. asperatus* C. E. Hubb., Hooker's Ic. Pl. t. 3337 (1937). -
Type: Queensland, Gregory North District, Duchess, collected in
February 1931, C. E. Hubbard 7348. - Holotype: K !, isotype: BRI, CANB
!.

(2) Plants perennial (short-lived); (3) caespitose. (4)
Flowering culms 20 to 46 cm tall (average 33.6); (5) erect; (6)
branched; (7) branches concentrated on the upper nodes; (8) not
disarticulating at the nodes; (9) nodes hairy; (10) internodes pilose.
(11) Mid-culm sheaths longer than their internodes (sheaths
overlapping); (12) hairy. (13) Ligule 0.6 to 0.8 mm long (average
0.75). (14) Leaf blades 3 to 9.5 cm long (average 5.5); (15) 1.6 to 4
mm wide (average 3.0); (16) involute; (17) surface antrorsely scabrous
(strongly so); (18) adaxially pilose; (19) abaxially pilose; (20)
apices not hair-like; (21) margins antrorsely serrulate. (22)
Inflorescence 1.2 to 6.2 cm long (average 3.7); (23) densely
contracted; (24) oblong to elliptic; (25) axillary inflorescence
present. (26) Cleistogamous spikelets present in axils of upper
sheaths only. (27) Spikelets about the same length throughout the
panicle; (28) 3.2 to 6 mm long (average 4.4); (29) ovate; (30) 3 to
4-flowered; (31) with 1 fertile floret; (32) sterile florets not
crowded distally; (33) sterile florets not reflexed. (34) Glumes
subequal; (35) pilose; (36) coriaceous; (37) green (straw-coloured at
maturity); (38) margins pale green; (39) apices erose; (40) not
concealed by overlapping awns. (41) Lower glume 2.4 to 4.8 mm long

(average 3.3); (42) 4 to 7-nerved; (43) truncate, or mucronate; (44) lanceolate to ovate. (45) Upper glume 2.8 to 5 mm long (average 3.6); (46) 5 to 6-nerved; (47) truncate, or mucronate; (48) elliptic. (49) Body of the lowest lemma 1.2 to 2.4 mm long (average 1.8); (50) 1 to 2.2 mm wide (average 1.7); (51) apex truncate to obtuse; (52) 9-nerved (rarely 11 to 13); (53) lacking extra nerves between main ones; (54) 1 nerve entering each peripheral awn; (55) surface shallowly ribbed; (58) yellow; (60) dorsally convex; (61) hairy on the lower part; (62) hairs longer, to as long as, the body; (63) margins ciliate; (64) normally lacking marginal hyaline lobes. (65) Body width to the length 0.6 to 0.9 (average 0.8). (66) Body length to the length of the awns 0.6 to 0.9 (average 0.7). (67) Awns 9; (68) 2 to 3.2 mm long (average 2.5); (69) subequal; (70) bases lacking a thickened ridge; (71) yellow; (72) inner rim of cilia present. (73) Palea of the lowest floret 1.6 to 3.6 mm long (average 2.3); (74) hairy between the nerves; (75) apex cleft; (76) apex hairy; (77) hairy on the flaps. (78) Rachilla between lower two florets without a hair tuft. (79) Lemma of the second floret not ribbed; (80) glabrous. (81) Anthers 0.4 to 1.2 mm long (average 0.9); (82) yellow. (83) Caryopsis 1 to 1.8 mm long (average 1.2); (84) 0.6 to 1 mm wide (average 0.8); (85) ellipsoid. (86) Embryo 0.6 to 0.8 the caryopsis length (average 0.7); (87) 0.7 to 1.2 mm long (average 0.9).

Distribution: Queensland. (Map 7)

Ecology: The species occurs in arid tussock and hummock grasslands and arid and semi-arid woodlands (Moore 1970). Associated species include *Eucalyptus argillacea*, *Cassia oligophylla*, *Triodia pungens*, *Triodia* spp., *Aristida* sp. and *Enneapogon* spp. Soils range from skeletal stony

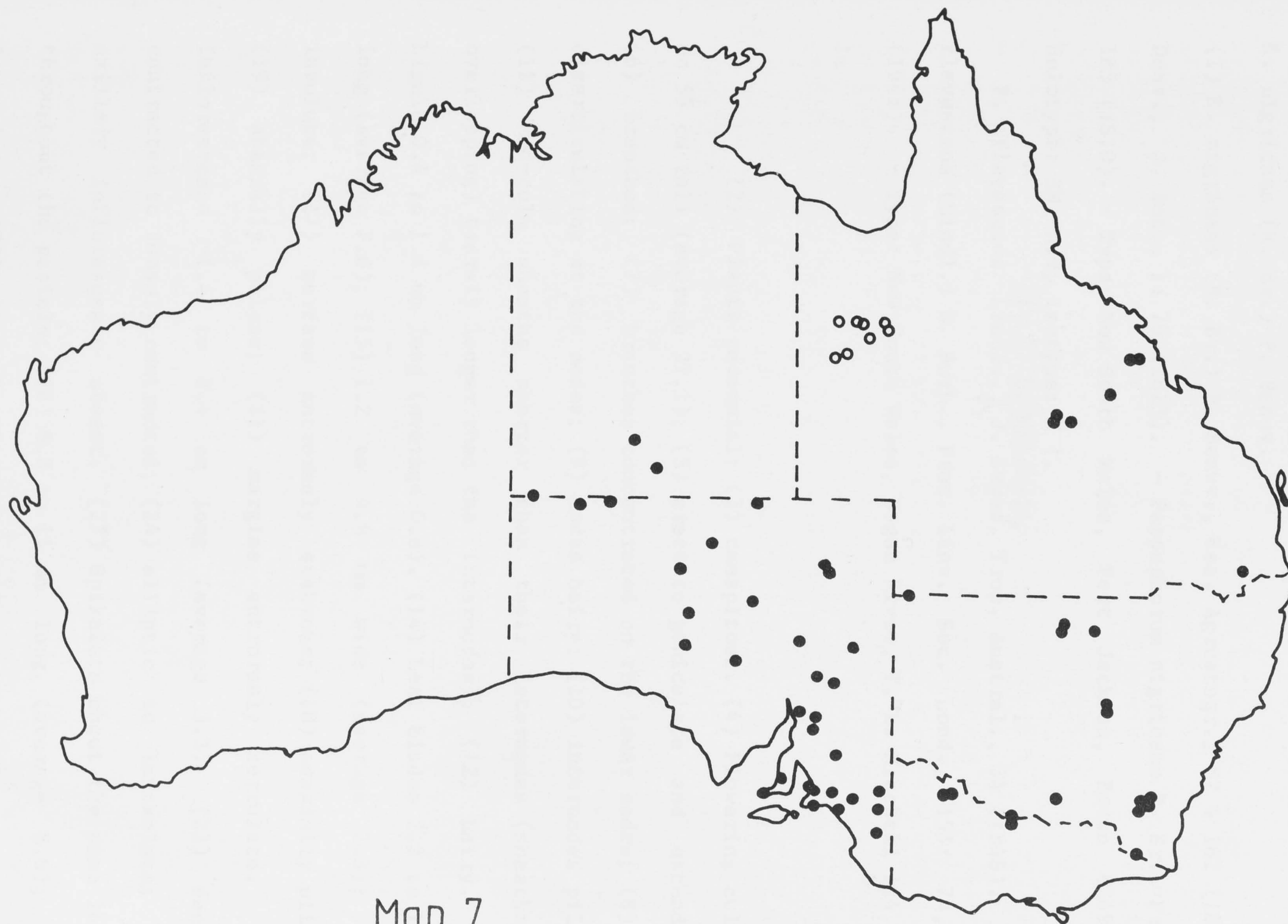
brown to red-brown sandy loams and shallow grey-brown calcareous desert types.

Representative specimens (13/28)

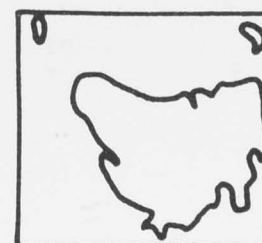
QUEENSLAND: Duchess, Hubbard 7348 (BRI CANB), Blake 11518 (BRI CANB); 13 miles S. W of Dajarra township, Lazarides 4048 (BRI CANB), 4049 (BRI); Ardmore, Everist 3205 (CANB); 10 miles S.E of Cloncurry, Lazarides 4413 (AD BRI CANB); 16 miles N. E of Cloncurry, Lazarides 4801 (AD BRI CANB); East Selwyn Range, 15 km W. of Cloncurry, Pullen 10404 (BRI CANB); 2 miles E. of Granada station, Lazarides 48004A (BRI CANB); 12 miles S. W of Malbon township, Lazarides 4017 (BRI CANB); between Mary Kathleen and Cloncurry, Beaumont & Modrak 7114 (BRI); Lake Moondarra road, 3 km from junction with Mount Isa - Camooweal road, Simon 2987 (BRI); 40 km E. of Mary Kathleen on Cloncurry road, Farrell 759 (BRI); no specific locality, Everist 3201 (BRI).

Reference: Burbidge (1941: 88)

Map 7. Distribution of *E. asperatus* (o) and *E. nigricans* (●).



Map 7



5.8.12. *E. nigricans*

E. nigricans (R. Br.) P. Beauv.

(1) *E. nigricans* (R. Br.) P. Beauv., Ess. Agrostogr., 82 & 162 (1812); Desv., J. Bot., 1: 70 (1813). - *Pappophorum nigricans* R. Br., Prod., 185 (1810). - Type: New South Wales, Port Jackson, Brown 6249. - Holotype: BM, n.v; isotype: K !.

- *P. flavescens* Lindl., ^{in T. L. Mitchell,} J. Exped. Trop. Austral., 34 (1848). - *E. flavescens* (Lindl.) N. Burb., Proc. Linn. Soc. Lond., 153: 74, 75 (1941). - Type: New South Wales, Bogan River, T. L. Mitchell 124, CGE !.

(2) Plants perennial; (3) caespitose. (4) Flowering culms 5 to 55 cm tall (average 27.1); (5) erect to geniculate and ascending; (6) branched; (7) branches concentrated on the lower nodes; (8) not disarticulating at the nodes; (9) nodes hairy; (10) internodes pilose. (11) Mid-culm sheaths shorter than their internodes (sheaths not overlapping) (rarely longer than the internodes); (12) hairy. (13) Ligule 0.4 to 1.4 mm long (average 0.6). (14) Leaf blades 2.2 to 18 cm long (average 7.6); (15) 1.2 to 4.8 mm wide (average 2.3); (16) involute; (17) surface antrorsely scabrous; (18) adaxially pilose; (19) abaxially pilose; (21) margins antrorsely serrulate. (22) Inflorescence 1.4 to 8.4 cm long (average 3.3); (23) densely contracted to loosely contracted; (24) elliptic to lanceolate; (25) axillary inflorescence absent. (27) Spikelets about the same length throughout the panicle; (28) 5.2 to 11 mm long (average 8.6); (29) lanceolate; (30) 4 to 5 -flowered; (31) with 1 fertile floret; (32) sterile florets not crowded distally; (33) sterile florets not

reflexed. (34) Glumes subequal; (35) pilose; (36) coriaceous; (37) grey; (38) margins pale green; (39) apices not erose; (40) not concealed by overlapping awns. (41) Lower glume 2.8 to 6.7 mm long (average 5.1); (42) 5 to 10 -nerved (average 6.7); (43) acute (rarely obtuse or acuminate); (44) lanceolate to ovate. (45) Upper glume 3.1 to 8 mm long (average 5.1); (46) 4 to 9-nerved; (47) acute to acuminate (rarely obtuse); (48) elliptic, or lanceolate to ovate. (49) Body of the lowest lemma 1.8 to 3.4 mm long (average 2.7); (50) 2 to 3.4 mm wide (average 2.4); (51) apex obtuse; (52) 9-nerved; (53) lacking extra nerves between main ones; (54) 1 nerve entering each peripheral awn; (55) surface shallowly ribbed; (57) papillose; (58) yellow to grey; (60) dorsally convex; (61) hairy on the lower part; (62) hairs as long as the body; (63) margins ciliate; (64) normally lacking marginal hyaline lobes. (65) Body width to the length 0.7 to 1.3 (average 1.0). (66) Body length to the length of the awns 0.4 to 0.6 (average 0.5). (67) Awns 9; (68) 4.2 to 7.8 mm long (average 6.3); (69) subequal; (70) bases lacking a thickened ridge; (71) yellow to grey; (72) inner rim of cilia present. (73) Palea of the lowest floret 2.2 to 3.5 mm long (average 3); (74) hairy between the nerves; (75) apex cleft; (76) apex hairy; (77) hairy on the flaps. (78) Rachilla between lower two florets without a hair tuft. (79) Lemma of the second floret not ribbed; (80) glabrous. (81) Anthers 0.8 to 1.4 mm long (average 1.0); (82) yellow. (83) Caryopsis 1.3 to 2.2 mm long (average 1.8); (84) 0.9 to 1.5 mm wide (average 1.2); (85) ellipsoid. (86) Embryo 0.7 to 0.9 the caryopsis length (average 0.8); (87) 1 to 1.8 mm long (average 1.4).

Remarks: Brown (1810) cited three localities for his collections: the south coast, Port Jackson and the north-eastern coast. Domin (1915)

cited Brown's specimens from Port Jackson in New South Wales and Keppel Bay, Queensland both bearing the same collection number 6249. Burbidge (1941) did not see the north-eastern specimen cited by Brown. She used the south coast specimen as the type for *E. nigricans*. The Keppel Bay specimen was separated as *E. arenicola* N. Burb. In his *Fragm.* 8: 200 (1872-74) Mueller included *E. nigricans* under *P. commune*, the name he suggested for all Australian material. Bentham, in his *Fl. Austral.*, 7: 600 (1878), included *P. gracilis* under *P. nigricans* while Domin revised it as *P. gracile* var. *Brownianum*, *Biblioth. Bot.*, 20: 381 (1915), based on Brown 6249.

Distribution: New South Wales and the Australian Capital Territory, Northern Territory, Queensland, South Australia and Victoria (Map 7)

Ecology: The species occurs commonly in sub-humid woodlands, semi-arid and arid shrublands, and tussock and hummock grasslands (Moore 1970), pine forests, dry sclerophyll forests, brigalow, *Danthonia* - *Stipa* grasslands, and *Aristida* - *Aira* grasslands. Associated species include *Eucalyptus tessellaris*, *E. populnea*, *Cassia* spp., *Bothriochloa decipiens*, *Heteropogon* sp., *Setaria* sp. Soils range from gravelly clay-alluvium to sandy alluvium, stony and sandy loams. The plants are commonly grazed by rabbits.

Representative specimens (45/192)

AUSTRALIAN CAPITAL TERRITORY: Black Mountain, Pullen 4255, 1284, 2085 (CANB); near Canberra Airport, Pullen 2962 (CANB); Capital Hill, Pullen & Galore 4652 (CANB); bank of Murrumbidgee River near Cotter junction, Campbell 61 (CANB); Tuggeranong road, Reiner 422 (CANB); Mount Tennent, Pullen 2912 (CANB); Tharwa, Blake 7527 (BRI).

NEW SOUTH WALES: Bogan River, Mitchell 124 (CGE); White Horse Flats,

S. W of Boroomba station, Pullen 2415 (CANB); Cocketgedong station, W. of Urana, D & I. Parer CANB 321759 (CANB); Delegate, Pullen 4468 (CANB).

NORTHERN TERRITORY: George Gill Range, Reedy Creek, Herb. Tate AD 96923016-5 (AD); Idracowra, Herb. Black AD 97037063 (AD); Running Waters, Herb. Black AD 97037063-2 (AD).

SOUTH AUSTRALIA: Ernabella Mission station, Coombe AD 95951096 (AD); head of valley, 8 km N. of Mungeranie Homestead, Lothian & Francis 322 (AD); 11 km W. of Leigh Creek, Lothian 1062 (AD); Peake station, Tate AD 97609592 (AD); Tarcoola, Herb. Black AD 97037063-3 (AD); 5 km N. of Baratta, Copley 3728 (AD CANB); Hope Valley, Smith 2165 (AD); Adelaide Plains, Kraehenbuehl 3513 (AD); Dover Gardens, Smith 2083 (AD); head of Spencer Gulf, Port Augusta, Cleland AD 97309218 (AD); Winnininnie, S. A. Pastoral Board AD 97629301, AD 97908023 (AD); N. of Yunta, Cole AD 96929387 (AD); Hundred of Wiltunga, Copley 37, 1854 (AD); 6 km W. of Snowtown on Bute road, Copley 179 (AD); 16 km N. of of Paruna, Copley (AD); Kinchina, Ising AD 96621145 (AD); Monarto New Town area, 15 km W. of Murray Bridge, Jackson 2504 (AD).

QUEENSLAND: between Toolbura and Rosehill, N. of Warwick, Hubbard 5643 (BRI CANB); Logan Downs, 22 km W. of Moranbah, Russell R24 (BRI); Alpha, Hubbard 7869 (BRI); 40 km S. E of Jericho, Beeston 1298C (BRI); 42 miles S. W of Nebo Township, Story & Yapp 33 (BRI CANB); 5 miles S. of Nebo, Story & Yapp 2 (CANB); 42 km N. W of Morven on road to Augathella, Purdie 314D (CANB).

VICTORIA: Echuca, Mueller CANB 258119 (CANB); 5 km S. W of Chinkapook, Beauglehole 55500 (BRI).

References: Bailey (1902); Black (1978: 186, fig. 144); Burbidge (1941: 76); Burbidge (1968: 114, pl. 42); Burbidge & Gray (1970: 43,

fig. 35); Cameron (1979: 174, fig. 53); Cunningham et al. (1981: 95, fig. 20e); Ewart (1930: 142); Gardner (1952: 32); Jacobs & Pickard (1981: 44); Jessop (1981: 445); Maiden (1898a: 104); Maiden (1898b: 142); Moore & Betche (1893: 485); Turner (1891: 26); Turner (1895: 45); Turner (1921: 19); Vickery (1953: 84); Willis (1970: 168).

5.8.13. *E. robustissimus*

E. robustissimus (Domin) N. Burb.

(1) *E. robustissimus* (Domin) N. Burb., Proc. Linn. Soc. Lond., 153: 78 (1941). - *Pappophorum nigricans* var. *robustissimum* Domin, Biblioth. Bot., 20: 381 (1915). - Type: Queensland, from Flinders River, Hughenden, collected in February 1910, Domin s.n. - Holotype: PR, n.v; isotype: K !.

(2) Plants perennial; (3) caespitose. (4) Flowering culms 50 to 107 cm tall (average 73.5); (5) erect; (6) branched; (8) not disarticulating at the nodes; (9) nodes hairy; (10) internodes villous. (11) Mid-culm sheaths longer than their internodes (sheaths overlapping), or shorter than their internodes (sheaths not overlapping); (12) hairy. (13) Ligule 0.6 to 1.2 mm long (average 0.9). (14) Leaf blades 6.5 to 22 cm long (average 14.6); (15) 3.8 to 6 mm wide (average 5.1); (16) flat to involute; (17) surface retrorsely scabrous; (18) adaxially pilose; (19) abaxially pilose to glabrous; (20) apices not hair-like; (21) margins retrorsely serrulate. (22) Inflorescence 2 to 9.3 cm long (average 4.1); (23) densely contracted;

(24) elliptic, or lanceolate (the general shape may be interrupted by longer branches); (25) axillary inflorescence absent. (27) Spikelets about the same length throughout the panicle; (28) 4.8 to 10 mm long (average 7.2); (29) lanceolate; (30) 5-flowered; (31) with 1 fertile floret; (32) sterile florets not crowded distally; (33) sterile florets not reflexed. (34) Glumes subequal; (35) pilose (often with stalked glandular hairs), or glabrous; (36) membranous; (37) green (straw-coloured at maturity); (38) margins pale green; (39) apices erose; (40) concealed by overlapping awns. (41) Lower glume 3 to 4.8 mm long (average 3.8); (42) 4 to 8-nerved (frequently 5-7); (43) truncate, or mucronate; (44) elliptic to lanceolate to ovate. (45) Upper glume 3.2 to 5.6 mm long (average 4.2); (46) 3 to 7-nerved (frequently 5-7); (47) truncate, or mucronate; (48) oblong to elliptic. (49) Body of the lowest lemma 2 to 3.6 mm long (average 2.7); (50) 1.6 to 2.9 mm wide (average 2.1); (51) apex truncate; (52) 9 to 11-nerved; (53) lacking extra nerves between main ones; (54) 1 to 2 nerves entering each peripheral awn; (56) surface ribbed on the upper part; (58) yellow; (60) dorsally convex; (61) hairy on the lower part; (62) hairs as long as, to shorter than, the body; (63) margins ciliate; (64) normally lacking marginal hyaline lobes. (65) Body width to the length 0.6 to 1 (average 0.7). (66) Body length to the length of the awns 0.4 to 0.8 (average 0.7). (67) Awns 9; (68) 2.8 to 6 mm long (average 4.5); (69) subequal; (70) bases lacking a thickened ridge; (71) yellow; (72) inner rim of cilia present. (73) Palea of the lowest floret 2.4 to 3.8 mm long (average 2.9); (74) hairy between the nerves; (75) apex cleft; (76) apex hairy; (77) hairy on the flaps. (78) Rachilla between lower two florets without a hair tuft. (79) Lemma of the second floret not ribbed; (80) glabrous. (81) Anthers 0.8

to 1.7 mm long (average 1.2); (82) yellow. (83) Caryopsis 1.5 to 2 mm long (average 1.7); (84) 0.8 to 1.4 mm wide (average 1.0); (85) obovoid to ellipsoid. (86) Embryo 0.4 to 0.8 the caryopsis length (average 0.5); (87) 1.1 to 1.6 mm long (average 1.3).

Affinities: The species is closely related to *E. arenicola* and *E. conicus*, but it differs by having strongly retrorsely scabrous leaves with retrorsely serrulate margins.

Distribution : Northern Territory and Queensland. (Map 8b)

Ecology: The species occurs in tropical and sub-tropical shrublands, semi-arid woodlands, and arid tussock grasslands (Moore 1970). Associated species include *Eucalyptus crebra*, *E. polycarpa*, *E. papuana*, *E. tetradonta*, *Acacia* spp., *Grewia* spp., *Hakea chordophylla*, *Grevillea striata*. Soils range from truncated lateritic types, sandy yellow and red podzolics to sandy clay loams. The plants are frequently found on river banks and dry river beds.

Representative specimens (28/36)

NORTHERN TERRITORY: Border Waterhole, Latz 1664 (BRI CANB); 60 miles N. N. E of Creswell station, Perry 1669 (CANB); 6 miles W. of Beswick station, Specht 1652 (AD); MacDonald Downs station, Chalmers 3 (AD); 40 miles E. of Daly Waters, Passlow NB 2564 (BRI).

QUEENSLAND: Gilbert River, Bick s.n 1914 (CANB); 2.5 km N. of Fairview on Peninsula Development road, Clarkson 3155 (BRI); Princess Charlotte Bay, Buckley 6329 (BRI); 4 miles N. of Lynd station, Lazarides 4172 (CANB); between Rockhampton and Westwood, White 3389 (BRI); 44 miles W. of Charlotte Plains station, Lazarides 4516 (CANB); Mount Isa, Winders 7410 (CANB); 18 km near the junction of Normanton,

Cloncurry and Julia Creek roads, Schmid 173 (CANB); 18 km E. of Mount Isa, Henderson H1863 (BRI); Torrens Creek, Hughenden, Latz 1644 (BRI); 20 km N. W of Tooluc on the Selwyn road, Purdie 1549 (BRI); Warena station, half-way between Winton and Boulia, Everist & Smith 116 (BRI); 13 km N. W of Moray Downs, Adams 1183 (BRI CANB); Belyando shire, 105 km N. N. W of Clermont, Epping Forest National Park, Gordon BRI 296271 (BRI); east shore of Lake Buchanan, 10 miles N. of Bowrie station, Adams 1165 (BRI); 10 miles E. N. E of Prarie township, Lazarides 3589 (BRI CANB); 40 km E. of Barcaldine on Capricorn Highway, Simon & Clarkson 2781 (BRI); 39 km S. W of Jericho, Beeston 1290C (BRI); Prairie - Aramac road, McDonald 2609 (BRI); 16 miles N. W of Longreach, Davidson 234 (BRI); Epping Forest National Park near Clermont, Wilkinson A10, A20 (BRI); no specific locality, Brass 1885 (CANB) and Everist 1408 (BRI).

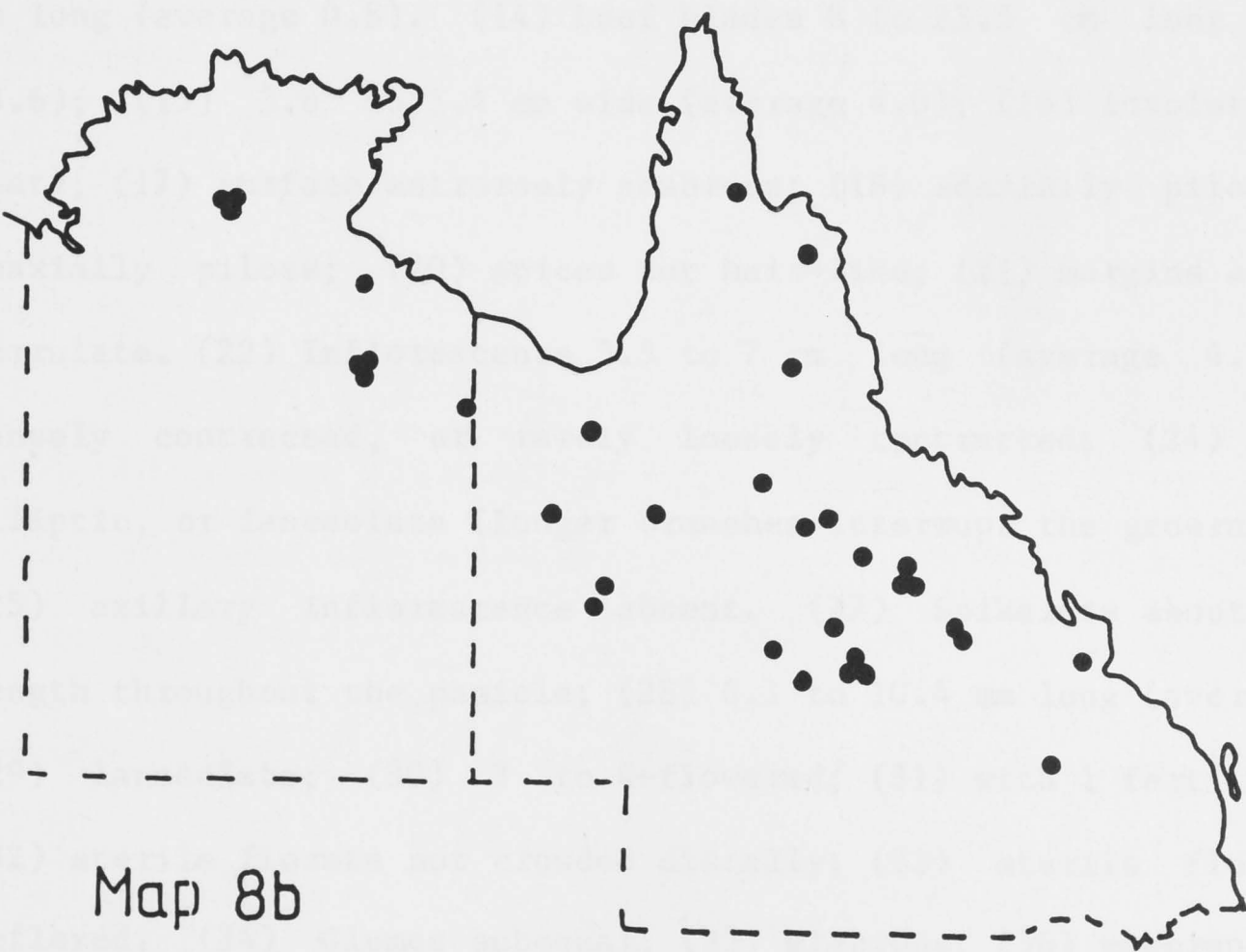
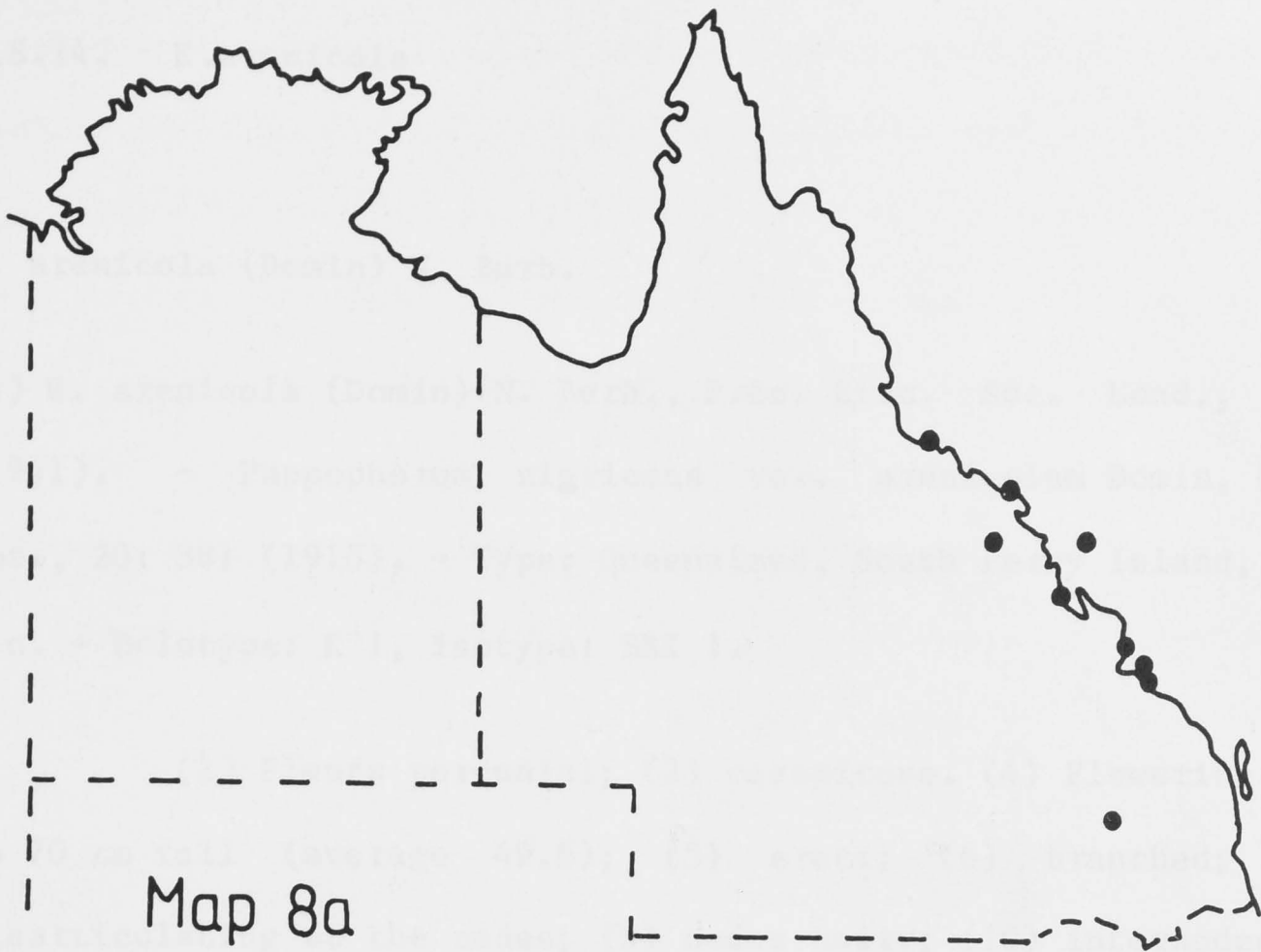
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Map 8b. Distribution of *E. robustissimus*.

Map 8a. Distribution of *E. arenicola*.



5.8.14. *E.arenicola*

E. arenicola (Domin) N. Burb.

(1) *E. arenicola* (Domin) N. Burb., Proc. Linn. Soc. Lond., 153: 77 (1941). - *Pappophorum nigricans* var. *arenicolum* Domin, Biblioth. Bot., 20: 381 (1915). - Type: Queensland, South Percy Island, H. Tryon s.n. - Holotype: K !, isotype: BRI !.

(2) Plants perennial; (3) caespitose. (4) Flowering culms 39 to 70 cm tall (average 49.6); (5) erect; (6) branched; (8) not disarticulating at the nodes; (9) nodes hairy; (10) internodes villous to pilose. (11) Mid-culm sheaths shorter (rarely longer) than their internodes (sheaths not overlapping); (12) hairy. (13) Ligule 0.6 to 1 mm long (average 0.8). (14) Leaf blades 8 to 23.5 cm long (average 13.6); (15) 3.6 to 5.4 mm wide (average 4.0); (16) involute (rarely flat); (17) surface antrorsely scabrous; (18) adaxially pilose; (19) abaxially pilose; (20) apices not hair-like; (21) margins antrorsely serrulate. (22) Inflorescence 3.5 to 7 cm long (average 4.7); (23) densely contracted, or rarely loosely contracted; (24) oblong to elliptic, or lanceolate (longer branches interrupt the general shape); (25) axillary inflorescence absent. (27) Spikelets about the same length throughout the panicle; (28) 6.1 to 10.4 mm long (average 8.5); (29) lanceolate; (30) 3 to 4-flowered; (31) with 1 fertile floret; (32) sterile florets not crowded distally; (33) sterile florets not reflexed. (34) Glumes subequal; (35) glabrous; (36) membranous; (37) green (straw-coloured at maturity); (38) margins pale green; (39) apices erose; (40) concealed by overlapping awns. (41) Lower glume 3.1 to 5 mm long (average 4.2); (42) 5 to 7-nerved (frequently 5); (43)

truncate to obtuse, or mucronate (rarely acute); (44) lanceolate to ovate. (45) Upper glume 3 to 5.8 mm long (average 4.7); (46) 3 to 6-nerved (frequently 5-6); (47) obtuse, or mucronate; (48) elliptic. (49) Body of the lowest lemma 2.2 to 3.2 mm long (average 2.1); (50) 1.6 to 2.5 mm wide (average 2.1); (51) apex truncate; (52) 9 to 11-nerved (each nerve entering an awn); (53) lacking extra nerves between main ones; (54) 1 nerve entering each peripheral awn; (56) surface ribbed on the upper part; (57) smooth; (58) yellow; (60) dorsally convex; (61) hairy on the lower part; (62) hairs as long as, to shorter than, the body; (63) margins ciliate; (64) lacking marginal hyaline lobes. (65) Body width to the length 0.6 to 0.9 (average 0.8). (66) Body length to the length of the awns 0.4 to 0.6 (average 0.5). (67) Awns 9 to 11; (68) 3.6 to 6.2 mm long (average 4.5); (69) subequal; (70) bases lacking a thickened ridge; (71) yellow to grey; (72) inner rim of cilia present. (73) Palea of the lowest floret 2.4 to 4 mm long (average 2.8); (74) hairy between the nerves; (75) apex cleft; (76) apex hairy; (77) hairy on the flaps. (78) Rachilla between lower two florets without a hair tuft. (79) Lemma of the second floret not ribbed; (80) glabrous. (81) Anthers 0.5 to 1.5 mm long (average 0.9); (82) yellow. (83) Caryopsis 1.6 mm long; (84) 0.6 to 0.9 mm wide (average 0.8); (85) obovoid to ellipsoid. (86) Embryo 0.5 to 0.8 the caryopsis length (average 0.6); (87) 0.8 to 1.2 mm long (average 1.0).

Affinities: The species is closely related to *E. robustissimus* but differs in having antrorsely scabrous leaf blades with antrorsely serrulate margins, and usually glabrous glumes.

Distribution: Eastern coast of Queensland and the nearby islands. (Map 8a)

Ecology: Mainly in tropical and sub-tropical forests and woodlands (Moore 1970), also *Spinifex hirsutus* open grasslands, and associated with *Helianthus argophyllus*.

Representative specimens (9/11)

QUEENSLAND: Chinchilla, Hubbard & Winders 6435 (CANB); 12 km N. of Cattle Port, 27 km S. of Yeppoon, Batianoff & McDonald 292 (BRI); Curtis Island, Queensland Naturalist Club s.n 22 iv 1962 (BRI); Bowen, Hubbard & Winders 6583 (CANB); Dingo Beach, Simon 3385 (BRI); Clair View, McDonald & Batianoff 1270 (BRI); Middle Percy Island, Tryon s.n 5 iii 1906 (BRI); Magnetic Island, Blake 8206 (CANB); Facing Island, Gladstone, Fitzsimon BRI 286832 (BRI).

5.8.15. *E. caerulescens*

E. caerulescens (Gaudich.) N. Burb.

(1) *E. caerulescens* (Gaudich.) N. Burb., Proc. Linn. Soc. Lond., 153: 87 (1941). - *Pappophorum caerulescens* Gaudich., Frey. Voy. Bot., 480 (1826). - Type: Western Australia, Sharks Bay, Gaudichaud s.n. - Holotype: P, n.v; isotype: BM, n.v, K ! (Burbidge 1941).

- *P. nigricans* var. *barbinode* Domin, J. Linn. Soc. London, Bot., 41: 227 (1912). - Type: Western Australia, between Ashburton and De Grey Rivers, Clement s.n, K !.

(2) Plants annual, or perennial; (3) caespitose. (4) Flowering culms 12 to 40 cm tall (average 23.4); (5) erect, or geniculate and ascending; (6) branched to unbranched; (7) branches

concentrated on the lower nodes; (8) not disarticulating at the nodes; (9) nodes hairy; (10) internodes villous to pilose. (11) Mid-culm sheaths longer than their internodes (sheaths overlapping), or shorter than their internodes (sheaths not overlapping); (12) hairy. (13) Ligule 0.4 to 1 mm long (average 0.6). (14) Leaf blades 2.3 to 12 cm long (average 6.0); (15) 1.4 to 3.5 mm wide (average 2.2); (16) flat or involute; (17) surface antrorsely scabrous; (18) adaxially pilose; (19) abaxially pilose; (20) apices not hair-like; (21) margins antrorsely serrulate. (22) Inflorescence 1 to 2.6 cm long (average 1.7); (23) densely contracted; (24) elliptic to lanceolate; (25) axillary inflorescence present. (26) Cleistogamous spikelets present in lower sheaths only. (27) Spikelets longer towards the panicle apex; (28) 3.8 to 10.6 mm long (average 6.8); (29) lanceolate; (30) 4 to 5-flowered; (31) with 1 fertile floret; (32) sterile florets not crowded distally; (33) sterile florets not reflexed. (34) Glumes subequal; (35) pilose; (36) coriaceous; (37) green to grey; (38) margins pale green; (39) apices erose; (40) not concealed by overlapping awns. (41) Lower glume 2.8 to 5.1 mm long (average 3.8); (42) 4 to 10-nerved (frequently 5-8); (43) truncate to obtuse; (44) lanceolate to ovate. (45) Upper glume 3 to 5.8 mm long (average 4.3); (46) 5 to 8-nerved; (47) truncate to obtuse; (48) elliptic. (49) Body of the lowest lemma 2 to 2.8 mm long (average 2.3); (50) 1.8 to 2.9 mm wide (average 2.3); (51) apex obtuse; (52) 10 to 13-nerved; (53) with or without extra nerves between main ones; (54) 1 to 2 nerve(s) entering each peripheral awn; (55) surface deeply ribbed; (57) papillose; (58) yellow to grey; (60) dorsally convex; (61) hairy on the lower part; (62) hairs longer than the body; (63) margins ciliate; (64) normally lacking marginal hyaline lobes. (65) Body width to the

length 0.7 to 1.3 (average 1.0). (66) Body length to the length of the awns 0.3 to 1 (average 0.6). (67) Awns 9; (68) 1.8 to 7.2 mm long (average 4.5); (69) subequal; (70) bases lacking a thickened ridge; (71) yellow to grey; (72) inner rim of cilia present. (73) Palea of the lowest floret 1.8 to 3.2 mm long (average 2.6); (74) hairy between the nerves; (75) apex cleft; (76) apex hairy (rarely glabrous); (77) hairy on the flaps; (78) Rachilla between lower two florets with a hair tuft, or without a hair tuft. (79) Lemma of the second floret not ribbed; (80) glabrous. (81) Anthers 0.6 to 1 mm long (average 0.7); (82) yellow. (83) Caryopsis 1.3 to 2 mm long (average 1.7); (84) 0.9 to 1.2 mm wide (average 1.1); (85) obovoid to ellipsoid. (86) Embryo 0.6 to 0.9 the caryopsis length (average 0.8); (87) 0.8 to 1.4 mm long (average 1.3).

Remarks: The species is capable of behaving as an annual when growing in well watered habitats, and such annuals approach a robust habit. Although it is characterized by the presence of cleistogenes in the axils of basal sheaths they are absent in the annuals (see Axillary cleistogamy).

Distribution: Northern Territory, South Australia, and Western Australia. (Map 9a)

Ecology: The species occurs mainly in shrub steppe, Acacia, and Eucalypt (Mallee) shrublands, and arid hummock grasslands (Moore 1970). Associated species include Acacia aneura, A. kempeana, A. sowdenii, Casuarina aristata over chenopods, Eucalyptus spp., Atriplex spp. and Maireana spp. Soils range from rocky and skeletal types on ridges and slopes to sands, loams and clays on flats. It is common in swales.

Representative specimens (27/147)

NORTHERN TERRITORY: The Sedimentaries, N. of Mount Olga, Latz 5454 (CANB); 25° 51' S 127° 42' E, Latz 5653 (CANB).

SOUTH AUSTRALIA: 126 miles N. of Cook, Symon 12713 (CANB); 104 km N. of Cook, Symon 12197 (BRI); Lyndhurst, Hill 22 (AD); Italowie Gorge, Cleland AD 96244001 (AD); 11 km W. of Leigh Creek, Lothian 1063 (AD); Yourambouka caves, S. of Hawker, Chinnock 304 (AD); near Blinman, Blake 16898 (BRI); Mount Parry, Tate AD 97609577 (AD); Lake Torrens, W. of Arcoona Dam, Cleland AD 96243467 (AD); Koonamore station, Orchard 200 (AD); 11 km N. E of Koonamore - Curnamona road, Baker 361 (AD); Koonamore Vegetation Reserve, Crisp 139 (AD); Quarry Hill, Koonamore, Osborne AD 97741268 (AD); 27 km N. of Maralinga, Lothian 5582 (AD); near Parakylia, Lake Parakylia, Lay 735 (AD).

WESTERN AUSTRALIA: Tunnel Creek, Prairie Downs, Mitchell 654 (CANB); 20 miles N. W of Belele Homestead, Speck 643 (AD CANB); near Lake Way, Craven (CANB); Buff Bore, 30 km S. E of Mount Vernon Homestead, upper Ashburton on banks of Ethel River, Mitchell 270 (CANB); shores of Lake Way, Craven 5106, 5121 (CANB); 70 miles E. N. E of Menzies, PERTH 1898 (PERTH); Roebourne, Neroman April 1923 (PERTH); 39.5 miles E. of Mount Magnet on road to Sandstone, Carr 483 (PERTH); Number One Well, Canning stock route, Craven 5069 (CANB).

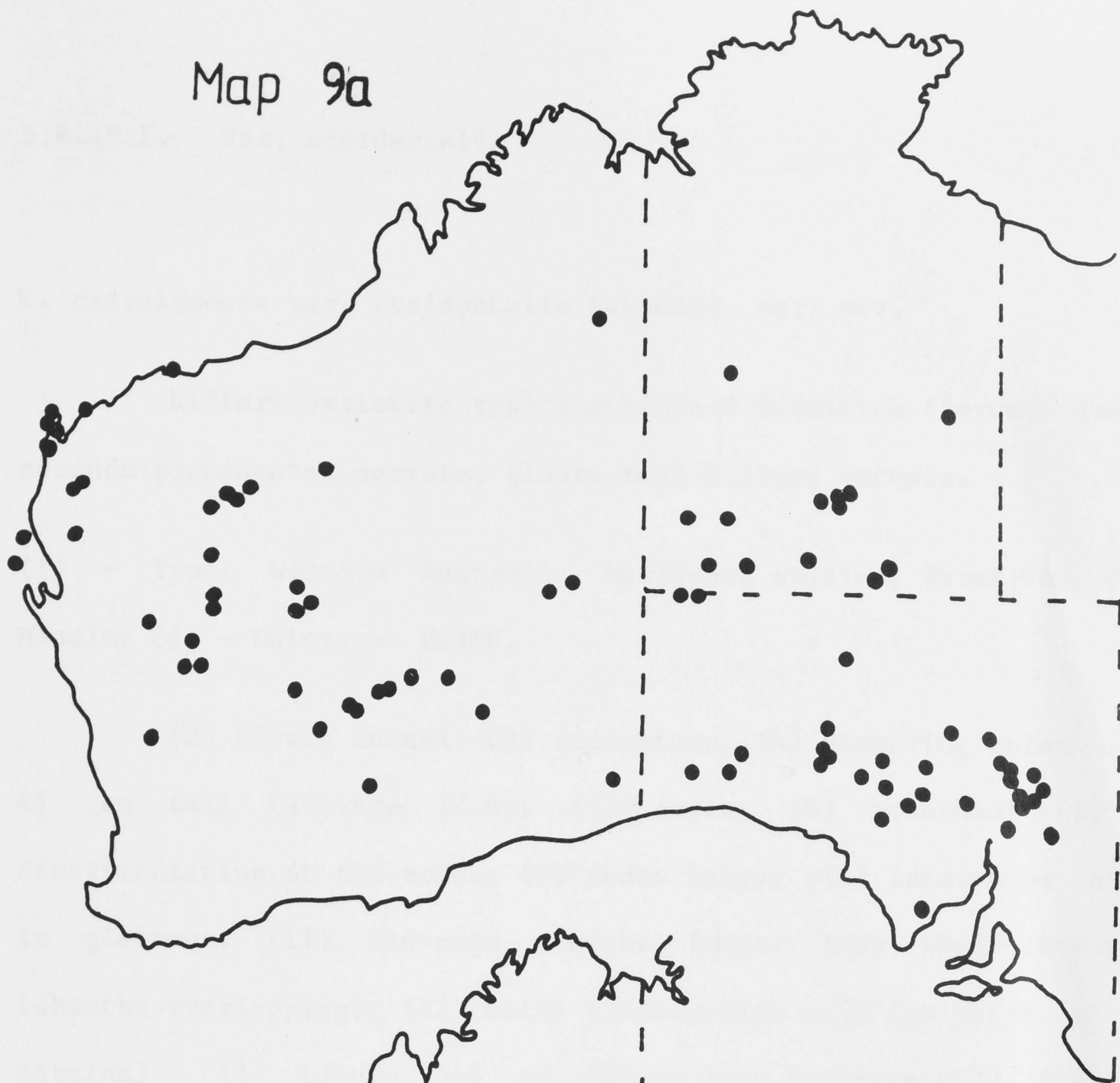
References: Black (1978: 185); Gardner (1952: 33); Jessop (1981:455).

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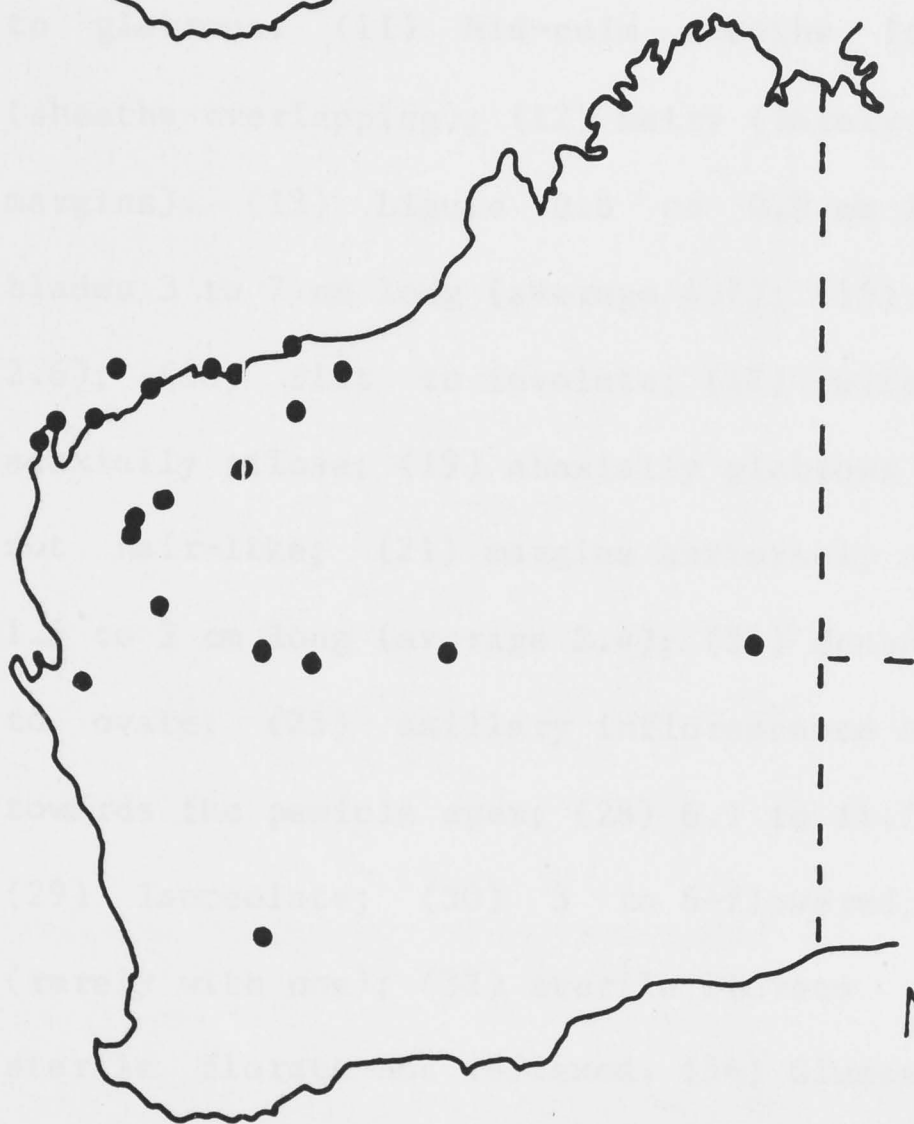
Map 9a. Distribution of *E. caeruleascens*.

Map 9b. Distribution of *E. caeruleascens* var. *occidentalis*.

Map 9a



Map 9b



5.8.15.1. Var. *occidentalis*

E. caerulescens var. *occidentalis* Kakudidi, var. nov.

Differt varietate typica spicula 2 fertilium florum, lemmate secunda prominenter nervata, glabra basi villosa excepta.

(1) - Type: Western Australia, Marijeron station, Carnarvon, G. R. Meadley 86. - Holotype: PERTH.

(2) Plants annual; (3) caespitose. (4) Flowering culms 8.5 to 45 cm tall (average 17.6); (5) erect; (6) branched; (8) not disarticulating at the nodes; (9) nodes hairy; (10) internodes pilose to glabrous. (11) Mid-culm sheaths longer than their internodes (sheaths overlapping); (12) hairy (rarely with only few hairs at the margins). (13) Ligule 0.6 to 0.8 mm long (average 0.7). (14) Leaf blades 3 to 7 cm long (average 4.7); (15) 1.7 to 3.6 mm wide (average 2.6); (16) flat to involute; (17) surface antrorsely scabrous; (18) adaxially pilose; (19) abaxially glabrous (rarely pilose); (20) apices not hair-like; (21) margins antrorsely serrulate. (22) Inflorescence 1.5 to 3 cm long (average 2.4); (23) densely contracted; (24) elliptic to ovate; (25) axillary inflorescence absent. (27) Spikelets longer towards the panicle apex; (28) 6.1 to 14.1 mm long (average 11.9); (29) lanceolate; (30) 3 to 6-flowered; (31) with 2 fertile florets (rarely with one); (32) sterile florets not crowded distally; (33) sterile florets not reflexed. (34) Glumes subequal; (35) pilose; (36) coriaceous; (37) green (straw-coloured at maturity); (38) margins pale green; (39) apices erose; (40) not concealed by overlapping awns. (41) Lower glume 4.7 to 7 mm long (average 5.7); (42) 8 to 15-nerved

(frequently 11); (43) truncate to obtuse; (44) lanceolate to ovate. (45) Upper glume 5.4 to 9.2 mm long (average 7.8); (46) 7 to 14-nerved; (47) truncate to obtuse; (48) elliptic, or lanceolate to ovate. (49) Body of the lowest lemma 2.7 to 4.1 mm long (average 3.5); (50) 2.2 to 3.4 mm wide (average 2.9); (51) apex truncate; (52) 9 to 11-nerved; (53) lacking extra nerves between main ones; (54) 1 to 2 nerve(s) entering each peripheral awn; (55) surface deeply ribbed; (57) papillose; (58) yellow; (60) dorsally straight; (61) hairy on the lower part; (62) hairs longer than the body; (63) margins ciliate; (64) lacking marginal hyaline lobes. (65) Body width to the length 0.7 to 1 (average 0.8). (66) Body length to the length of the awns 0.4 to 0.7 (average 0.6). (67) Awns 9; (68) 5.2 to 10 mm long (average 7.4); (69) subequal; (70) bases lacking a thickened ridge; (71) yellow, or purplish-pink; (72) inner rim of cilia present. (73) Palea of the lowest floret 3 to 3.8 mm long (average 3.4); (74) hairy between the nerves; (75) apex cleft; (76) apex glabrous; (77) hairy on the flaps. (78) Rachilla between lower two florets with a hair tuft. (79) Lemma of the second floret ribbed; (80) hairy on the lower part. (81) Anthers 0.4 to 0.7 mm long (average 0.5); (82) yellow. (83) Caryopsis 1.6 to 2.3 mm long (average 2.0); (84) 1.1 to 1.4 mm wide (average 1.3); (85) globoid to ellipsoid. (86) Embryo 0.8 to 0.9 the caryopsis length; (87) 1.3 to 1.7 mm long (average 1.65).

Remarks: Burbidge (1941) commented on two forms. She noted some specimens had purplish awns whereas in the rest of the material they were black or straw coloured, and that a few specimens had a rather robust habit and larger glumes. The specimens with purplish awns, robust habit and larger glumes have been included in the variety.

Affinities: The variety is distinguished from the typical one by having 2 fertile florets per spikelet and a hairy ribbed second lemma.

Distribution: Western Australia. (Map 9b).

Ecology: The variety occurs mainly in Acacia (Mulga) shrublands (Moore 1970), and mulga and spinifex. Associated species include Acacia aneura, A. grasbyi, A. tetragonophylla, A. victoriae, Eremophila sp., Eucalyptus microtheca, Paspalidium clementii, Enneapogon sp., Triodia sp., Sporobolus australasicus, Aristida contorta, etc. It is common on sandy soils.

Representative specimens (20/27)

WESTERN AUSTRALIA: 4.5 miles N. of Yardie Creek, George 6676 (PERTH); Roebourne, Gardner s.n 1932 (PERTH); Mardie station, Black s.n 7 v 1976 (PERTH); Locker Island, Onslow, Goodall 598 (PERTH); Abydos Research Station S. of Port Hedland, Stone 2 (PERTH); Warralong station, Burbidge 799, 893 (PERTH); S. of Desert Well near Wiluna, Melville 331 (PERTH); Barrow Island, Buckley 6801 (PERTH); Dalgety Brook, Cransfield 2056 (PERTH); 5 km near Tom Price township, Pilbara region, Pullen 10944A (CANB); 5 miles E. of Belele station, Speck 619 (CANB); 7 km E. of Jameson Settlement, Latz 7653 (CANB); Woodstock station, Pilbara, Ealey 142 (PERTH); Mount Herbert, S. S. E of Roebourne, George 3499 (PERTH); Wongawal station, Bennett 68 (PERTH); Egnibah station, Burbidge 1022 (PERTH); Marijeron station near Carnarvon, Meadley 86 (PERTH); Ashburton, 38 km from Ullawarra station, Simon & Stretch 3765 (BRI); Ashburton, 26 km from Ullawarra station, Simon & Stretch 3761 (BRI); Ashburton, 33 km from Minnie Creek station, on road to Edmund station, Simon & Stretch 3749 (BRI); Ashburton, 19 km from Minnie Creek station on road to Edmund station,

Simon & Stretch 3740 (BRI).

5.8.16. *E. cylindricus*

E. cylindricus N. Burb.

(1) *E. cylindricus* N. Burb., Proc. Linn. Soc. Lond., 153: 89 (1941).

- Type: South Australia, Frome Downs, Wade 26, K, n.v.

(2) Plants perennial; (3) caespitose. (4) Flowering culms 10 to 51 cm tall (average 24.1); (5) erect; (6) branched; (8) disarticulating at the nodes; (9) nodes hairy; (10) internodes pilose. (11) Mid-culm sheaths longer than their internodes (sheaths overlapping), or shorter than their internodes (sheaths not overlapping); (12) hairy. (13) Ligule 0.6 to 1 mm long (average 0.8). (14) Leaf blades 3.1 to 15 cm long (average 8.6); (15) 2.2 to 5.2 mm wide (average 2.9); (16) involute; (17) surface antrorsely scabrous; (18) adaxially pilose; (19) abaxially pilose; (20) apices not hair-like; (21) margins antrorsely serrulate. (22) Inflorescence 3.1 to 14 cm long (average 8.0); (23) densely contracted; (25) axillary inflorescence present. (26) Cleistogamous spikelets present in upper and lower sheaths. (27) Spikelets about the same length throughout the panicle; (28) 4.8 to 8.6 mm long (average 6.7); (29) lanceolate; (30) 3 to 4-flowered; (31) with 1 fertile floret; (32) sterile florets not crowded distally; (33) sterile florets not reflexed. (34) Glumes subequal; (35) pilose; (36) coriaceous; (37) green (straw-coloured at maturity); (38) margins pale green; (39) apices erose; (40) not

concealed by overlapping awns. (41) Lower glume 2.9 to 5.6 mm long (average 4.0); (42) 5 to 8-nerved (frequently 7); (43) truncate to acute; (44) lanceolate to ovate. (45) Upper glume 3.2 to 5.4 mm long (average 4.8); (46) 4 to 8-nerved (frequently 5); (47) truncate to obtuse; (48) elliptic. (49) Body of the lowest lemma 1.9 to 3.2 mm long (average 2.5); (50) 1.5 to 2.9 mm wide (average 2.1); (51) apex truncate to obtuse; (52) 9 to 11-nerved; (53) lacking extra nerves between main ones; (54) 1 to 2 nerve(s) entering each peripheral awn; (55) surface deeply ribbed to shallow ribbed; (57) papillose; (58) yellow to grey; (60) dorsally convex; (61) hairy on the lower part; (62) hairs longer than, to hairs as long as, the body; (63) margins ciliate; (64) normally lacking marginal hyaline lobes. (65) Body width to the length 0.7 to 1 (average 0.8). (66) Body length to the length of the awns 0.5 to 1 (average 0.6). (67) Awns 9 or rarely 11; (68) 2.2 to 5.4 mm long (average 3.8); (69) subequal; (70) bases lacking a thickened ridge; (71) yellow to grey; (72) inner rim of cilia present. (73) Palea of the lowest floret 2 to 3.6 mm long (average 2.9); (74) hairy between the nerves; (75) apex cleft; (76) apex glabrous; (77) hairy on the flaps. (78) Rachilla between lower two florets without a hair tuft. (79) Lemma of the second floret not ribbed; (80) glabrous. (81) Anthers 0.4 to 1.8 mm long (average 1.0); (82) yellow. (83) Caryopsis 1.4 to 2.1 mm long (average 1.6); (84) 0.8 to 1.1 mm wide (average 0.9); (85) obovoid to ellipsoid. (86) Embryo 0.7 to 0.9 the caryopsis length (average 0.8); (87) 1 to 1.6 mm long (average 1.2).

Distribution: New South Wales, Northern Territory, Queensland, South Australia, and Western Australia. (Map 10)

Ecology: The species occurs in shrub steppe and Acacia shrublands, and

arid hummock grasslands (Moore 1970), also Cassia - Acacia woodland and Chenopod low shrublands. Associated species include *Acacia aneura*, *A. georginae*, *A. kempeana*, *A. ligulata*, *Eucalyptus* sp., *Eremophila* sp., *Aristida contorta*, and *Enneapogon* spp. Soils range from light brown to grey clays, deep red fine sandy loams, red-brown loose calcareous sands, to gravelly and limestone types. The plants behave as ephemerals and grow in watercourses, swampy areas and lake shores.

Representative specimens (43/196)

QUEENSLAND: close to Queensland - Northern Territory border, Blake 1756 (CANB); between Santos - Orientos stations, Martensz s.n CANB 321740 (CANB).

NEW SOUTH WALES: Mount Mulyah, Moore 5808 (CANB); Pelora, Moore 5220 (CANB); Tero Creek station, Martensz CANB 321743 (CANB); Airstrip, Fowlers Gap, 70 miles N. of Broken Hill, Vasek 68719-49 (CANB). Mount Murchison station, Wilcannia, Bailey CANB 321742 (CANB); Tundulyah, Moore 5596 (CANB); Calindary station, N. W of White Cliffs, Hall CANB 321741 (CANB); 5 miles S. W of Quarry View Homestead, Vasek 680803-21A (CANB).

NORTHERN TERRITORY: Mount Gillen, 8 km W. S. W of Alice Springs, Pullen 10.457 (CANB); Deep Well road, 15.5 miles S. of Alice Springs, Nelson 209 (CANB); 1.5 miles W. of Argadargada, Chippendale 2930 (BRI CANB); 10 miles E. of Undoolya station, Perry 3265 (CANB); Tanami Desert Wildlife Sanctuary, near Chillawells bore, Beauglehole 50639 (CANB); 17 miles N. W of Andado Homestead, Must, 57 (CANB); N. W of Simpson Desert, Latz 4651 (BRI CANB); 4 miles N. of Erldunda Homestead, Winkworth 74 (CANB); 31 miles N. of Alice Springs, Nelson 1874 (CANB); 4 miles S. of Tempe Downs Homestead, Chippendale CANB 33282 (CANB); 9.5 miles N. N. W of Alice Springs, Lazarides 5173

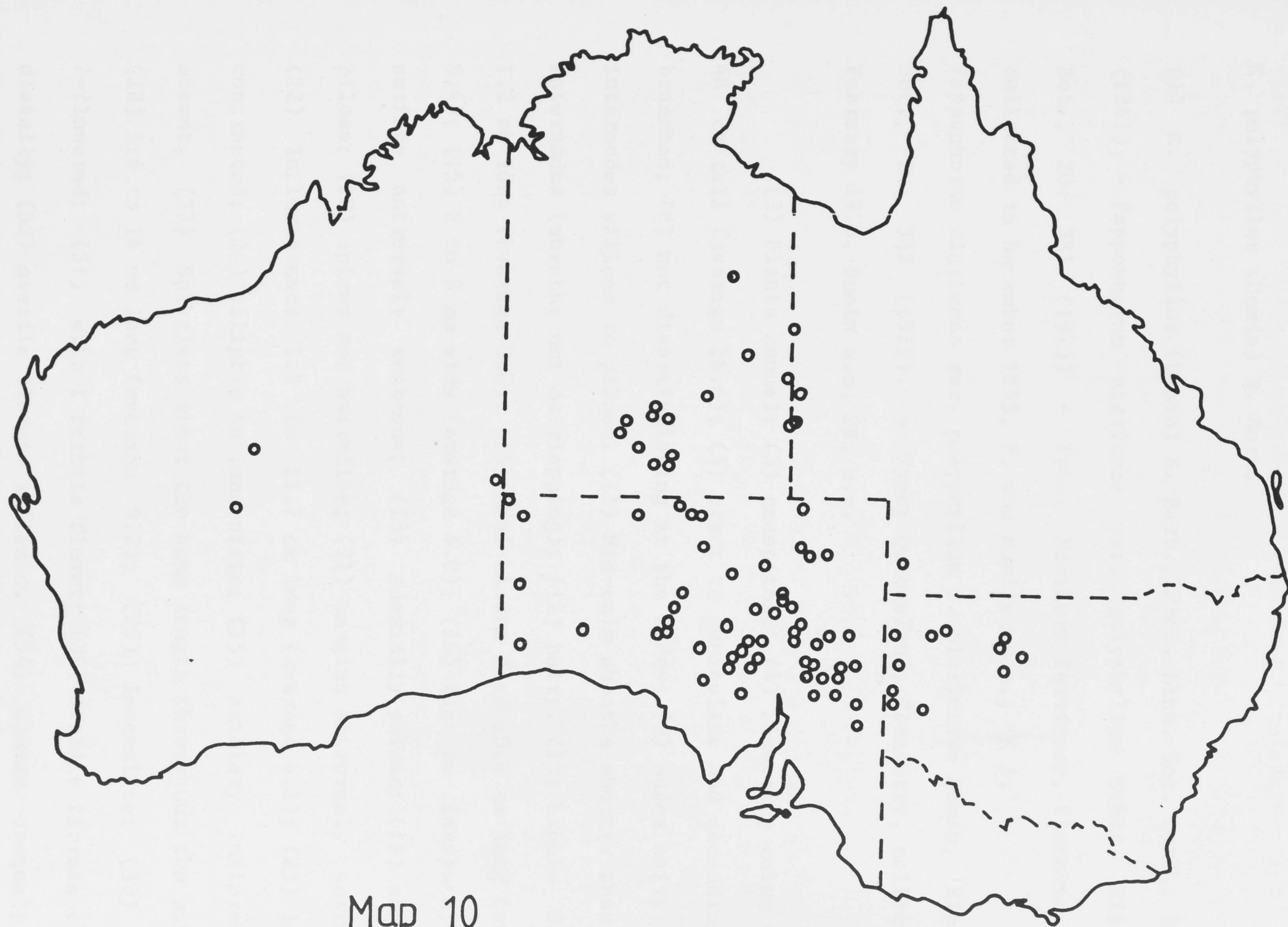
(CANB); New Haven station Latz 2130 (CANB); High River crossing, 5 miles S. W of Jays Creek, S. W of Alice Springs, Burbidge & Gray 4244 (CANB); near Alroy Downs station, Blake 17885 (CANB); 9 miles S. E of Undoolya, Perry 3256a (CANB); flat top hill 5 km S. W of Huckitta outstation, Parker 232 (CANB); 10 miles S. E of Ringwood, Schofield CANB 123494 (CANB); 39.5 miles S. W of Tobermory Homestead, Chippendale 2972 (AD CANB).

SOUTH AUSTRALIA: 15 miles N. of Maralinga, Perry 5562 (CANB); Arcoona, Murry 209 (CANB); 58 km N. W of William Creek railway siding on road to Oodnadatta, Lazarides 8190A (CANB); Yudnapinna station, Port Augusta, Burbidge CANB 15319 (CANB); Woomera East, Patterson CANB 20455 (CANB); Birdsville Track, Filson 3296 (AD); Ross River crossing near Ludgates well, Shaw 495 (AD); Durkin outstation, 15 km W. of Mulgathing, Weber 2820 (CANB); Andamooka, Williams 2814 (AD); Roxby Downs, Aitken 15, 37 (AD); 1 km W. of Nepabunna, Whibley 3878 (AD); 11 km W. of Leigh Creek, Lothian 1062 (AD); 16 km N. of Quondong Vale, Williams 7793 (AD); Curnamona, Cleland AD 96243446 (AD); Belleroo Creek, E. N. E of Frome Downs Homestead, Whibley 3457 (AD).

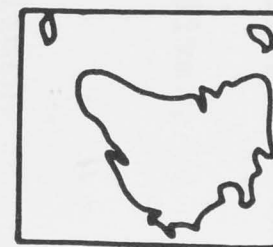
WESTERN AUSTRALIA: Pindini, Helms 6 (PERTH); Lake Violet station, Wiluna, Bennett 61 (PERTH); Giles area on the Western Australia - Northern Territory border, Cleland AD 9794163 (AD).

References: Black (1978: 186); Burbidge (1941: 89, fig. 5) Cameron (1979: 165); Cunningham et al. (1981: 93, fig. 20b) Gardner (1952: 33); Jacobs & Pickard (1981: 44); Jessop (1981: 455, fig: 580C) Lazarides (1970: 120: pl. 33b); Vickery (1953: 84).

Map 10. Distribution of *E. cylindricus*.



Map 10



5.8.17. *E. polyphyllus*

E. polyphyllus (Domin) N. Burb.

(1) *E. polyphyllus* (Domin) N. Burb., Proc. Linn. Soc. Lond., 153: 69 (1941), - *Pappophorum nigricans* var. *polyphyllum* Domin, Biblioth. Bot., 20: 381 (1915) - Type: Northern Territory, Victoria River, collected in December 1855, F. von Mueller s.n., K !.

Pappophorum nigricans var. *polyphyllum* f. *plurinerve* Domin, Biblioth. Bot., 20: 382 (1915). - Type: Queensland, Cloncurry, collected in February 1910, Domin s.n, PR, n.v.

(2) Plants annual; (3) caespitose. (4) Flowering culms 4.5 to 48 cm tall (average 26.6); (5) erect to geniculate and ascending; (6) branched; (8) not disarticulating at the nodes; (9) nodes hairy; (10) internodes villous to pilose. (11) Mid-culm sheaths shorter than their internodes (sheaths not overlapping); (12) hairy. (13) Ligule 0.4 to 1.2 mm long (average 0.8). (14) Leaf blades 3 to 15.6 cm long (average 8.4); (15) 2 to 6 mm wide (average 4.0); (16) flat to involute; (17) surface antrorsely scabrous; (18) adaxially pilose; (19) abaxially pilose; (20) apices not hair-like; (21) margins antrorsely serrulate. (22) Inflorescence 1.5 to 11.7 cm long (average 6.2); (23) loosely contracted; (24) elliptic to lanceolate; (25) axillary inflorescence absent. (27) Spikelets about the same length throughout the panicle; (28) 5.6 to 14 mm long (average 9.2); (29) lanceolate; (30) 5 to 7-flowered; (31) with 1 fertile floret; (32) sterile florets crowded distally; (33) sterile florets reflexed. (34) Glumes unequal; (35) pilose; (36) coriaceous; (37) green to grey; (38) margins pale green to purplish; (39) apices not erose; (40) not concealed by overlapping

awns. (41) Lower glume 4.2 to 8.2 mm long (average 6.0); (42) 6 to 13-nerved (frequently 8-11); (43) acute to acuminate; (44) lanceolate to ovate. (45) Upper glume 4.3 to 9.2 mm long (average 6.9); (46) 5 to 11-nerved (frequently 5-8); (47) acute to acuminate; (48) elliptic, or lanceolate to ovate. (49) Body of the lowest lemma 2 to 4.2 mm long (average 3.1); (50) 1.4 to 3.8 mm wide (average 2.5); (51) apex obtuse; (52) 9 to 11-nerved; (53) lacking extra nerves between main ones; (54) 1 to 2 nerve(s) entering each peripheral awn; (56) surface ribbed on the upper part, or not ribbed; (57) papillose; (58) yellow to grey; (60) dorsally convex; (61) hairy on the lower part; (62) hairs longer than the body; (63) margins glabrous; (64) lacking marginal hyaline lobes. (65) Body width to the length 0.6 to 1.1 (average 0.8). (66) Body length to the length of the awns 0.3 to 0.9 (average 0.5). (67) Awns 9; (68) 3 to 11.6 mm long (average 6.2); (69) subequal; (70) bases lacking a thickened ridge; (71) yellow to grey; (72) inner rim of cilia present. (73) Palea of the lowest floret 2.2 to 3.7 mm long (average 2.4); (74) hairy between the nerves; (75) apex cleft; (76) apex glabrous; (77) hairy on the flaps. (78) Rachilla between lower two florets without a hair tuft. (79) Lemma of the second floret not ribbed; (80) glabrous. (81) Anthers 0.4 to 1.4 mm long (average 0.7); (82) yellow. (83) Caryopsis 1.3 to 2 mm long (average 1.8); (84) 1.1 to 1.5 mm wide (average 1.2); (85) obovoid to ellipsoid. (86) Embryo 0.6 to 0.9 the caryopsis length (average 0.8); (87) 1 to 1.7 mm long (average 1.4).

Remarks: Domin's type specimen at K was examined and found to agree with the specimen, Hubbard 7169, illustrated by Burbidge (1941). The latter was erroneously cited as 7769 among her representative specimens. However, there is another specimen of Mueller's at MEL

collected from the Victoria River in December 1855, which does not agree with the type of *E. polyphyllus*, but rightly belongs to *E. purpurascens*. Burbidge's (1941) illustration, Fig. 2, p. 71, was based on C. E. Hubbard & C. W. Winders 7169 collected from Queensland, Burke District, Jardine Valley (BRI, CANB). *E. polyphyllus* is characterized by the sterile florets crowded distally and reflexed.

Distribution: N. W of New South Wales, Northern Territory, Queensland, South Australia, and Western Australia. (Map 11)

Ecology: The species has a wide occurrence from tropical heaths, sub-tropical, tropical and semi-arid woodlands, shrublands, and arid tussock and hummock grasslands, to northern coastal grasslands (Moore 1970). Associated species include *Eucalyptus* spp., *Acacia* spp., *Casuarina* spp., *Bauhinia* spp., *Cassia* spp., *Dodonaea* spp., *Aristida* spp., *Enneapogon* spp., annual *Sorghum*, *Heteropogon* spp., *Themeda* spp., *Cenchrus* spp., and *Eragrostis* spp. Soils are also variable ranging from fine to coarse textured sands and clays on river, creek beds and alluvial plains to clay loams and desert sands, skeletal soils on ridges and rocky cliffs to limestone outcrops, and saline sands near salt lakes and the coast, etc.

Representative specimens (45/587)

NEW SOUTH WALES: Tundulyah, Moore 4831, 4801, 5740, 5724, 4867 (CANB); Tero Creek station, Martensz NT4538 (CANB); Broken Hill, Morris 10 (BRI), Ising AD 96032529 (AD).

NORTHERN TERRITORY: 45 miles S. W of Mongrel Downs Homestead, Latz 719 (CANB); 2.7 miles S. W of Glen Helen Homestead, Perry 8653 (CANB); 8 miles S. E of Angas Downs station, Winkworth 81 (BRI CANB); Alice Springs, Lazarides 5320 (BRI CANB), Sim AD 96803664 (AD) and Ryko AD

97947294 (AD); 21 miles N. E of Argadargada station, Lazarides 6220 (CANB); King's Canyon, Latz 298 (AD CANB); 14 miles S. W of Narweitooma station Homestead, Maconochie 26 (AD CANB); Haast's Bluff Mission, Cleland AD 97215057 (AD); October creek, Passlow 78 (BRI); 4 miles from CSIRO Reseach Station, Katherine, Adams 1702 (CANB).

QUEENSLAND: 8 miles N. E of Dajarra township, Lazarides 4352 (CANB); 9 miles S. E of Dajarra township, Lazarides 4330 (AD CANB); Comet, Hubbard 7971 (BRI); 11 km N. W of Charters Towers on Lynd road, Simon 3444 (BRI); at junction of Broughton and Burdekin roads, Hubbard & Winders 6995 (BRI); Betoota, Blake 12174 (BRI); Cunnamulla, Hubbard & Winders 6252 (BRI); Charleville, Black 11026 (BRI); Longreach, Rocklea, Sutherland 13 (BRI); Chillagoe, Hubbard & Winders 6832 (BRI); East Selwyn Ranges, 15 km W. of Cloncurry, Pullen 10403 (CANB); Debessile, 20 miles N. of Hughenden, Tothill H145 (BRI); Dugald River, 40 km N. W of Cloncurry, Beaumont 7024, 7048 (CANB); Granada, Everist 5230 (BRI); Nonda between Hughenden and Cloncurry, Hubbard & Winders 7231 (BRI).

SOUTH AUSTRALIA: 16 miles W. of South Australia - Queensland border, between Innamincka and Nappamerry, Symon 5754A (CANB); Hamilton Homestead, Badman 236 (AD); Mount Gason, Crocker AD 97609580 (AD); Mount Morris, Mann Ranges, Symon 2619 (AD); Yaundun station near Hawker Gate, Martensz s.n 8 viii 1966 (CANB); W. of Mount Wedge, Nichols 811 (CANB).

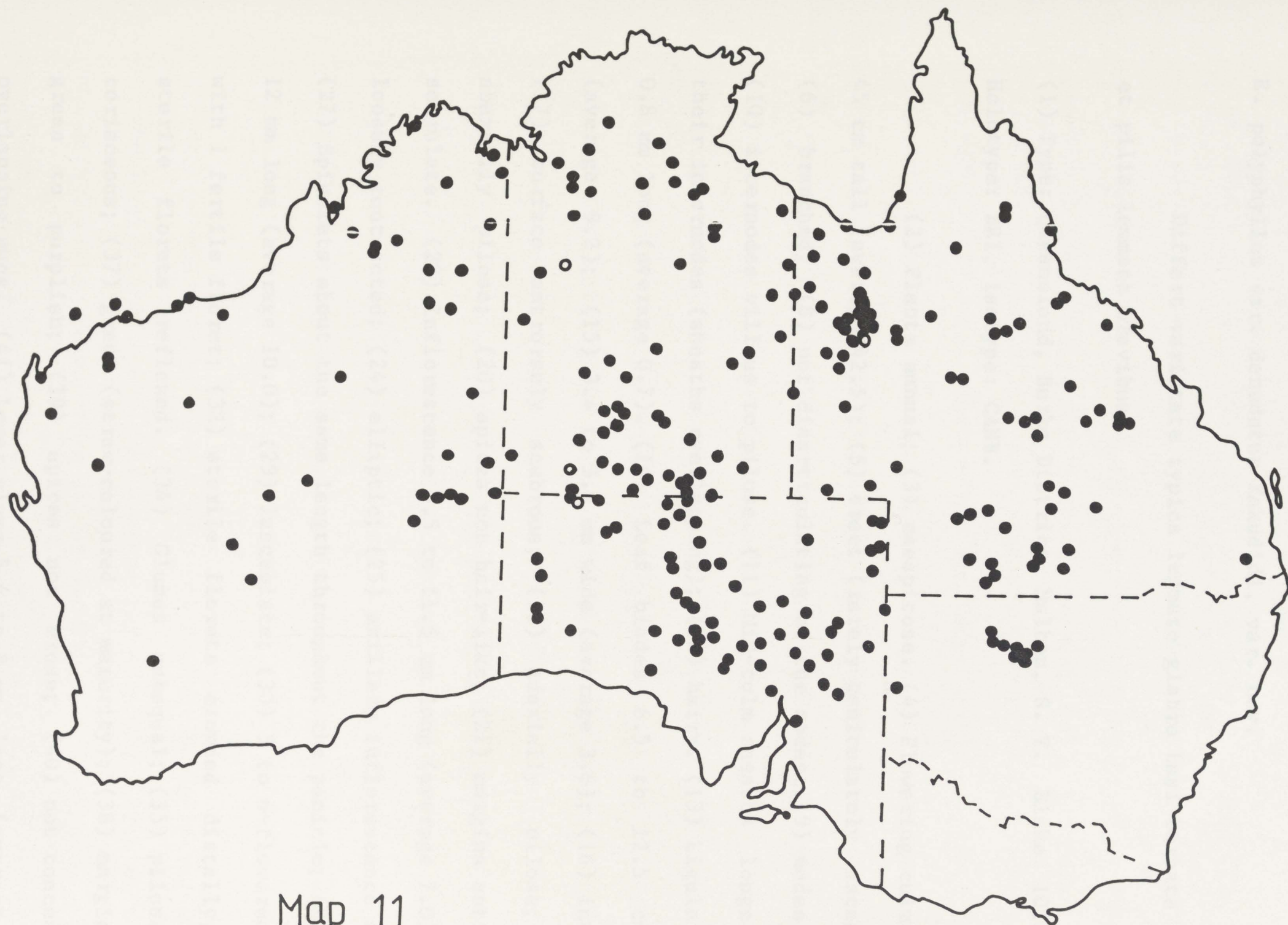
WESTERN AUSTRALIA: Mount Connor, Carr & Beauglehole 45620 (CANB); Giles, Chippendale NT4554 (CANB); Karunjie station, Rust 33 (CANB); Dampier Archipelago, Legendre Island, Royce 7289 (CANB).

References: Black (1978: 187, fig. 145); Burbidge (1941: 69, fig. 2); Cameron (1979: 182); Cunningham et al. (1981: 94, fig. 20g); Jacobs &

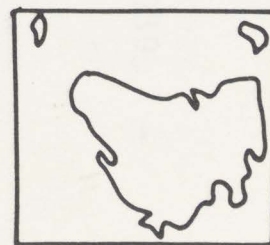
Pickard (1981: 44); Jessop (1981: 453, fig. 580b); Lazarides (1970: 126, pl. 33c); Vickery (1953: 84).

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Map 11. Distribution of *E. polyphyllus* (●) and var. *denudatus* (○).



Map 11



5.8.17.1. Var. denudatus

E. polyphyllus var. *denudatus* Kakudidi, var. nov.

Differt varietate typica lemmate glabro basi barbata excepta et pilis lemmate brevibus.

(1) Type: Queensland, Burke District, Malbon, S. T. Blake 101039. -
Holotype: BRI, isotype: CANB.

(2) Plants annual; (3) caespitose. (4) Flowering culms 30 to 45 cm tall (average 42.5); (5) erect (rarely geniculately ascending); (6) branched; (8) not disarticulating at the nodes; (9) nodes hairy; (10) internodes villous to pilose. (11) Mid-culm sheaths longer than their internodes (sheaths overlapping); (12) hairy. (13) Ligule 0.6 to 0.8 mm long (average 0.7). (14) Leaf blades 6.5 to 12.5 cm long (average 9.2); (15) 3.4 to 3.8 mm wide (average 3.6); (16) involute; (17) surface antrorsely scabrous; (18) adaxially pilose; (19) abaxially pilose; (20) apices not hair-like; (21) margins antrorsely serrulate. (22) Inflorescence 5.5 to 11.5 cm long (average 7.0); (23) loosely contracted; (24) elliptic; (25) axillary inflorescence absent. (27) Spikelets about the same length throughout the panicle; (28) 9 to 12 mm long (average 10.0); (29) lanceolate; (30) 5 to 6-flowered; (31) with 1 fertile floret; (32) sterile florets crowded distally; (33) sterile florets reflexed. (34) Glumes subequal; (35) pilose; (36) coriaceous; (37) green (straw-coloured at maturity); (38) margins pale green to purplish; (39) apices not erose; (40) not concealed by overlapping awns. (41) Lower glume 5.4 to 8 mm long (average 6.8); (42) 9 to 12-nerved; (43) acuminate; (44) lanceolate to ovate. (45)

Upper glume 7.2 to 8.4 mm long (average 7.4); (46) 5-nerved; (47) acute to acuminate; (48) elliptic, or lanceolate to ovate. (49) Body of the lowest lemma 3 to 3.4 mm long (average 3.2); (50) 3 to 3.3 mm wide (average 3.2); (51) apex obtuse; (52) 9-nerved; (53) lacking extra nerves between main ones; (54) 1 nerve entering each peripheral awn; (56) surface ribbed on the upper part, or not ribbed; (57) papillose; (58) yellow; (60) dorsally convex; (61) glabrous (except for a tuft of hairs at the base, and occasionally with sparse hairs on the back); (62) hairs shorter than the body; (63) margins glabrous; (64) lacking marginal hyaline lobes. (65) Body width to the length 0.7 to 1 (average 0.9). (66) Body length to the length of the awns 0.4 to 0.6 (average 0.5). (67) Awns 9; (68) 6 to 8.6 mm long (average 7.2); (69) subequal; (70) bases lacking a thickened ridge; (71) yellow to purplish-pink; (72) inner rim of cilia present. (73) Palea of the lowest floret 2.7 to 3.4 mm long (average 3.0); (74) hairy between the nerves; (75) apex cleft; (76) apex glabrous; (77) hairy on the flaps. (78) Rachilla between lower two florets without a hair tuft. (79) Lemma of the second floret not ribbed; (80) glabrous. (81) Anthers 0.8 to 1.1 mm long (average 0.9); (82) yellow. (83) Caryopsis 1.8 to 2 mm long (average 1.9); (84) 1.2 to 1.4 mm wide (average 1.3); (85) obovoid. (86) Embryo 0.7 to 0.8 the caryopsis length (average 0.77); (87) 1.4 to 1.5 mm long (average 1.45).

Affinities: The variety differs from the typical one by being glabrous on the body of the lower lemma (except for a tuft of hairs at the base and occasionally sparse hairs at the back).

Distribution: Northern Territory, Queensland and South Australia. (Map 11)

Ecology: The soils range from sandy gravel on creek frontages to stony ridges and limestone outcrops.

Representative specimens (4/4)

NORTHERN TERRITORY: Carrara creek, Latz 1665 (BRI, CANB); Ayers Rock, north side, Donner (AD).

QUEENSLAND: Malbon, Blake 10139 (BRI CANB).

SOUTH AUSTRALIA: Upsan Downs in Musgrave Ranges, Cleland s.n 20 iv 1950 (AD).

5.8.18. *E. intermedius*

E. intermedius N. Burb.

(1) *E. intermedius* N. Burb., Proc. Linn. Soc. Lond., 153: 67, 68 (1941). - Type: Queensland, Alpha, C. E. Hubbard 7881. - Holotype: K !, isotype: BRI !.

- *Pappophorum nigricans* var. *glabrescens* Domin, Biblioth. Bot., 20: 381 (1915). - Type: Queensland, Barcaldine, collected in March 1910, Domin s.n. - Syntype: PR, n.v; isosyntype: K !.

(2) Plants perennial; (3) caespitose. (4) Flowering culms 30 to 70 cm tall (average 49); (5) erect; (6) branched; (8) not disarticulating at the nodes; (9) nodes hairy; (10) internodes pilose. (11) Mid-culm sheaths longer than their internodes (sheaths overlapping), or shorter than their internodes (sheaths not overlapping); (12) hairy, or glabrous. (13) Ligule 0.6 to 1.4 mm long (average 0.9). (14) Leaf blades 8 to 27 cm long (average 15.3); (15)

3.2 to 6 mm wide (average 4.2); (16) involute; (17) surface antrorsely scabrous; (18) adaxially pilose; (19) abaxially glabrous (rarely pilose); (20) apices not hair-like; (21) margins antrorsely serrulate. (22) Inflorescence 3.1 to 13.5 cm long (average 6.9); (23) densely contracted, or loosely contracted; (24) oblong to elliptic, or lanceolate (general shape sometimes interrupted by longer branches); (25) axillary inflorescence absent. (27) Spikelets about the same length throughout the panicle; (28) 6.1 to 13 mm long (average 9.5); (29) lanceolate; (30) 3 to 5-flowered; (31) with 2 fertile florets; (32) sterile florets not crowded distally; (33) sterile florets not reflexed. (34) Glumes subequal; (35) pilose; (36) coriaceous; (37) green, or grey; (38) margins pale green; (39) apices erose, or not erose; (40) not concealed by overlapping awns. (41) Lower glume 3.5 to 7 mm long (average 5.5); (42) 7 to 16-nerved (frequently 7-11); (43) truncate to acute; (44) lanceolate to ovate. (45) Upper glume 4.5 to 8.5 mm long (average 6.3); (46) 6 to 11 -nerved (frequently 7-8); (47) truncate to obtuse (rarely acute); (48) elliptic, or lanceolate to ovate. (49) Body of the lowest lemma 2.2 to 3.6 mm long (average 2.9); (50) 2 to 3.2 mm wide (average 2.6); (51) apex obtuse; (52) 9-nerved (rarely 11-nerved); (53) lacking extra nerves between main ones; (54) 1 nerve entering each peripheral awn (or 2 if 11-nerved); (56) surface ribbed on the upper part; (57) papillose; (58) yellow (rarely grey); (60) dorsally convex; (61) hairy on the lower part; (62) hairs longer than the body (rarely as long as body); (63) margins ciliate; (64) normally lacking marginal hyaline lobes. (65) Body width to the length 0.7 to 1 (average 0.9). (66) Body length to the length of the awns 0.4 to 0.7 (average 0.5). (67) Awns 9; (68) 3.6 to 9 mm long (average 7.2); (69) subequal; (70) bases lacking a thickened ridge; (71) yellow

to grey; (72) inner rim of cilia present. (73) Palea of the lowest floret 2.2 to 3.6 mm long (average 2.9); (74) hairy between the nerves; (75) apex cleft; (76) apex hairy; (77) hairy on the flaps. (78) Rachilla between lower two florets without a hair tuft. (79) Lemma of the second floret not ribbed; (80) hairy on the lower part (occasionally glabrous). (81) Anthers 0.8 to 1.6 mm long (average 1.0); (82) yellow. (83) Caryopsis 1.5 to 2.2 mm long (average 1.8); (84) 1 to 1.6 mm wide (average 1.3); (85) obovoid to ellipsoid. (86) Embryo 0.7 to 1 the caryopsis length (average 0.8); (87) 1.2 to 1.8 mm long (average 1.4).

Distribution: New South Wales, Northern Territory, Queensland, South Australia, and Western Australia. (Map 12a)

Ecology: The species occurs mainly in semi-arid and arid woodlands, Acacia shrublands, arid tussock and hummock grasslands (Moore 1970). Associated species include Eucalyptus populnea, E. melanophloia, Acacia spp., A. aneura, Albizia basaltica, Callitris columellaris, Eragrostis lacunaria, Digitaria sp., Heteropogon contortus, Aristida ingrata, Cenchrus ciliaris, Triodia longiceps, and Enneapogon spp. Soils range from red-brown to grey-brown desert sands, sandy loams and red-brown silty loams.

Representative specimens (23/81)

NEW SOUTH WALES: along road between White Cliffs and Tero Creek station, Martensz 4488 (CANB); Tero Creek station, Martensz CANB 321753 (CANB).

NORTHERN TERRITORY: Umbeara station, Goyder creek, Latz 6902 (BRI CANB); Alice Springs, White AD 97734414 (AD); Simpson Gap National Park, Latz 8562 (BRI CANB); Motel Ayers Rock, Latz 8560 (BRI).

QUEENSLAND: 5 km E. of Barcaldine on the Capricorn Highway, Simon & Clarkson 2770 (CANB); 95 miles S. E of Charleville, Dingwall, Everist 3339 (CANB); 24 km E. of Barcaldine on the Capricorn Highway, Simon & Clarkson 2774 (BRI CANB); Gilruth Plains, Cunnamulla, Barker CANB 321752 (CANB) Alpha, Hubbard 7881 (BRI); 20 miles N. E of Duchess township, Latz 4393 (CANB); Cashel Vale S. of Bollon, Everist 2689 (BRI); Boatman station, Everist 2841 (BRI).

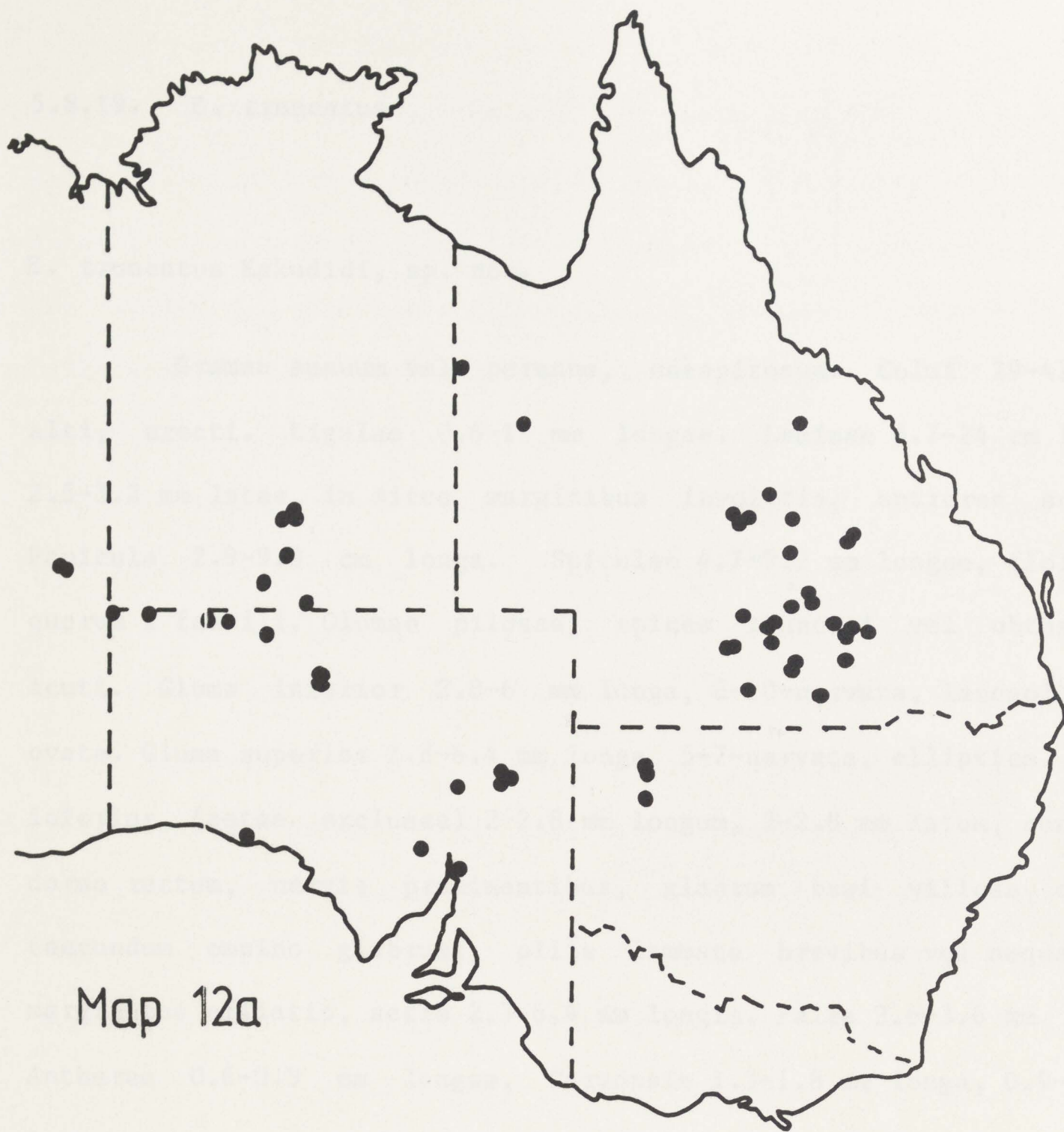
SOUTH AUSTRALIA: grown at the Waite Institute, Dolling CANB 266111 (CANB); Tomkinson Ranges, Cleland AD 97222268 (AD); Mann Ranges, 30 miles N. E of Mount Davies Camp, Latz 911 (CANB); Yudnapinna station, Port Augusta, Burbidge CANB 16577 (CANB); Ernabella, S. A Pastoral Board AD 9762934 (AD); N. W of Ernabella, Black AD 97637396 (AD); Arckaringa station, Henshall 3182 (CANB); eastern end of Musgrave Ranges, Ernabella, Turvey AD 97628089 (AD); western end of Musgrave Ranges, Cleland AD 97215043 (AD).

References: Cunningham et al. (1981: 95, fig. 20d); Jacobs & Pickard (1981: 44); Vickery (1953: 84).

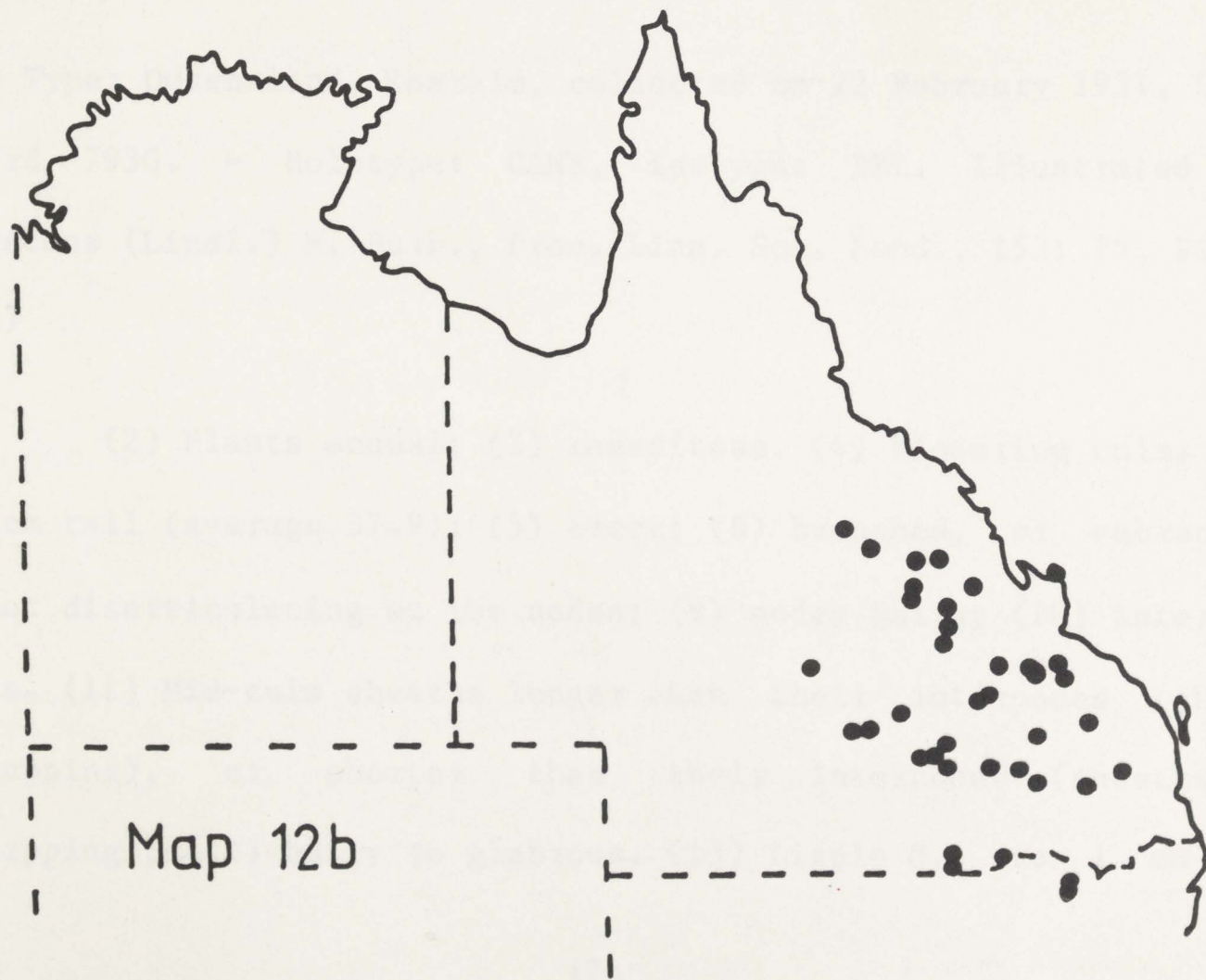
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Map 12a. Distribution of *E. intermedius*.

Map 12b. Distribution of *E. truncatus*.



Map 12a



Map 12b

5.8.19. *E. truncatus*

E. truncatus Kakudidi, sp. nov.

Gramen annuum vel perenne, caespitosum. Culmi 29-47.5 cm alti, erecti. Ligulae 0.6-1 mm longae. Laminae 6.7-24 cm longae, 2.5-3.2 mm latae, in sicco marginibus involutis, antrorse scabrae. Panicula 2.9-9.8 cm longa. Spiculae 4.7-9.2 mm longae, floribus 4 quorum 1 fertili. Glumae pilosae; apices truncati vel obtusi vel acuti. Gluma inferior 2.8-6 mm longa, 8-10-nervata, lanceolata vel ovata. Gluma superior 2.8-6.4 mm longa, 5-7-nervata, elliptica. Lemma inferius (setae exclusae) 2-2.8 mm longum, 2-2.8 mm latum, cuneatum, dorso rectum, nervis prominentibus, glabrum basi villosa excepta (secundum omnino glabrum), pilis lemmate brevibus vel aequalibus, marginibus ciliatis, setis 2.3-6.4 mm longis. Palea 2.6-3.6 mm longa. Antherae 0.6-0.9 mm longae. Caryopsis 1.3-1.8 mm longa, 0.9-1.1 mm lata.

(1) - Type: Queensland, Emerald, collected on 22 February 1931, C. E. Hubbard 7930. - Holotype: CANB, isotype: BRI. Illustrated as *E. flavescens* (Lindl.) N. Burb., Proc. Linn. Soc. Lond., 153: 75, Fig. 3 (1941)

(2) Plants annual; (3) caespitose. (4) Flowering culms 29 to 47.5 cm tall (average 37.9); (5) erect; (6) branched, or unbranched; (8) not disarticulating at the nodes; (9) nodes hairy; (10) internodes pilose. (11) Mid-culm sheaths longer than their internodes (sheaths overlapping), or shorter than their internodes (sheaths not overlapping); (12) hairy to glabrous. (13) Ligule 0.6 to 1 mm long

(average 0.9). (14) Leaf blades 6.7 to 24 cm long (average 12.4); (15) 2.5 to 3.2 mm wide (average 3.0); (16) involute; (17) surface antrorsely scabrous; (18) adaxially pilose; (19) abaxially glabrous; (20) apices not hair-like; (21) margins antrorsely serrulate. (22) Inflorescence 2.9 to 9.8 cm long (average 6.4); (23) densely contracted to loosely contracted; (24) lanceolate to linear; (25) axillary inflorescence absent. (27) Spikelets about the same length throughout the panicle; (28) 4.7 to 9.2 mm long (average 6.4); (29) ovate; (30) 4-flowered; (31) with 1 fertile floret; (32) sterile florets not crowded distally; (33) sterile florets not reflexed. (34) Glumes subequal; (35) pilose; (36) membranous; (37) green (straw-coloured at maturity); (38) margins pale green; (39) apices not erose; (40) not concealed by overlapping awns. (41) Lower glume 2.8 to 6 mm long (average 4.2); (42) 8 to 10-nerved; (43) truncate to acute; (44) lanceolate to ovate. (45) Upper glume 2.8 to 6.4 mm long (average 4.8); (46) 5 to 7-nerved; (47) truncate to acute; (48) elliptic. (49) Body of the lowest lemma 2 to 2.8 mm long (average 2.5); (50) 2 to 2.8 mm wide (average 2.6); (51) apex truncate; (52) 9 to 11-nerved; (53) with extra nerves between main ones; (54) 1 nerve entering each peripheral awn (extra nerves often adjacent to median nerve); (55) surface deeply ribbed; (57) smooth; (58) yellow; (59) cuneate; (60) dorsally straight; (61) hairy on the lower part; (62) hairs shorter than the body (rarely as long as body); (63) margins ciliate; (64) normally lacking marginal hyaline lobes. (65) Body width to the length 0.8 to 1 (average 0.9). (66) Body length to the length of the awns 0.4 to 0.8 (average 0.6). (67) Awns 9 to 10 (rare); (68) 2.3 to 6.4 mm long (average 4.0); (69) subequal; (70) bases lacking a thickened ridge; (71) yellow; (72) inner rim of cilia present. (73)

Palea of the lowest floret 2.6 to 3.6 mm long (average 3.1); (74) hairy between the nerves; (75) apex cleft; (76) apex hairy; (77) hairy on the flaps. (78) Rachilla between lower two florets without a hair tuft. (79) Lemma of the second floret not ribbed; (80) glabrous. (81) Anthers 0.6 to 0.9 mm long (average 0.7); (82) yellow. (83) Caryopsis 1.3 to 1.8 mm long (average 1.6); (84) 0.9 to 1.1 mm wide (average 1.0); (85) globoid to ellipsoid. (86) Embryo 0.75 to 0.87 the caryopsis length (average 0.79); (87) 1 to 1.4 mm long (average 1.3).

Remarks: The species was included by Burbidge (1941) in *E. flavescens* (Lindl.) N. Burb., but examination showed its type to be *E. nigricans*, of which *E. flavescens* therefore becomes a synonym. Burbidge seemed to have based the description of *E. flavescens* on the figured specimen, Hubbard 7930, which is distinct from Mitchell's specimen, the type chosen by Lindley. Hubbard 7930 has been nominated the type for *E. truncatus*.

Affinities: The species is distinguished from the allied *E. gracilis* and *E. virens* by having a deeply ribbed, dorsally straight lemma which appears cuneate.

Distribution: Southeastern Queensland and northeastern New South Wales. (Map 12b).

Ecology: The species occurs commonly in tropical and sub-tropical rain forests, brigalow forests, tropical and sub-tropical sub-humid woodlands, and semi-arid shrub woodlands (Moore 1970). Associated species include *Eucalyptus orgadophila*, *E. dichromophloia*, *Acacia farnesiana*, *A. harpophylla*, *A. cambagei*, *Terminalia oblongata*, *Astrebla lappacea*, *A. squarrosa*, *Astrebla* spp., *Dichanthium affine*, *D.*

sericeum, *Bothriochloa decipiens*, *Thellungia advena*, *Aristida* spp., *Digitaria divaricatissima*, *Enneapogon* spp., and *Melaleuca* spp. Soils range from heavy brown clays to dark clay loams.

Representative specimens (19/75)

NEW SOUTH WALES: 12 miles from Coolatai on road to Warialda, Morrow 103 (BRI CANB).

QUEENSLAND: on Bedourie road, 5 miles S. of Dawson Highway, Speck 1833 (CANB); 10 miles N. of Emerald township, Story & Yapp 189 (BRI CANB); Moray Downs Homestead, Story & Yapp 143 (BRI CANB); Barwon Park, Broadsound shire, Anderson 2064 (BRI); 30 km S. W of Moranbah, Brady 67 (BRI); Blair Athol, Blake 8054 (BRI); Blackall, Springer BRI 286605 (BRI); Biddenham W. of Augathella, Everist 3585 (BRI); Moray Downs, Jacobsen E613 (CANB); Urella, Belyando shire, Jacobsen E587 (BRI); Callide Research Station, Biloela, Cowdry 50 (BRI); Narine, S. E of Dirranbandi, Blake 10723 (BRI); Wallumbilla, Blunden 11 (BRI); Mundubbera, Bloxsome 29 (BRI); MacAlister, Hubbard & Winders 6461 (BRI); Noondoo, Cameron 13 (BRI); Limborne, Bailey BRI 266684 (BRI); Capella on Hamberstone road, Simon & Bisset 2877 (BRI).

References: Burbidge: (1941: 74, fig. 3); Cameron (1979: 167); Cunningham et al. (1981: 93, fig. 20c); Vickery (1953: 84); all as *E. flavescens*.

5.8.20. *E. conicus*

E. conicus Kakudidi, sp. nov.

Gramen perenne, caespitosum. Culmi 35-80 cm alti, erecti. Ligulae 0.6-1.2 mm longae. Laminae 8.5-26 cm longae, 2.4-5.4 mm latae, in sicco marginibus involutis, antrorse vel retrorse scabrae. Panicula 1.5-6 mm longa. Spiculae 4.4-10.8 mm longae. Glumae apices erosi. Gluma inferior 2.2-5.5 mm longa, 4-9-nervata, lanceolata vel ovata. Gluma superior 2.8-6.3 mm longa, 3-7-nervata, oblonga vel elliptica. Lemma inferius (setae exclusae) 2-3.3 mm longum, 1.4-2.9 mm latum, nervis prominentibus, dorso convexum, glabrum basi villosa excepta (secundum omnino glabrum), pilis lemmate aequalibus, marginibus ciliatis, setis 2.1-8mm longis. Palea 2.2-3.6 mm longa. Antherae 0.8-2.1 mm longae. Caryopsis 1.2-2.2 mm longa, 0.8-1.3 mm lata.

(1) - Type: Northern Territory, 27 miles E. of Docker River settlement, Latz 852. - Holotype: CANB, isotype: NT.

(2) Plants perennial; (3) caespitose. (4) Flowering culms 35 to 80 cm tall (average 56.7); (5) erect; (6) branched; (8) not disarticulating at the nodes; (9) nodes hairy; (10) internodes villous. (11) Mid-culm sheaths longer than their internodes (sheaths overlapping), or shorter than their internodes (sheaths not overlapping); (12) hairy. (13) Ligule 0.6 to 1.2 mm long (average 0.9). (14) Leaf blades 8.5 to 26 cm long (average 12.6); (15) 2.4 to 5.4 mm wide (average 4.3); (16) involute; (17) surface antrorsely scabrous, or retrorsely scabrous; (18) adaxially pilose; (19) abaxially glabrous; (20) apices not hair-like; (21) margins antrorsely

serrulate. (22) Inflorescence 1.5 to 6 cm long (average 3.6); (23) densely contracted; (24) oblong, or lanceolate; (25) axillary inflorescence absent. (27) Spikelets about the same length throughout the panicle; (28) 4.4 to 10.8 mm long (average 6.4); (29) lanceolate; (30) 4 to 5-flowered; (31) with 1 fertile floret (rarely with 2 fertile florets); (32) sterile florets not crowded distally; (33) sterile florets not reflexed. (34) Glumes subequal; (35) pilose; (36) membranous; (37) green (straw-coloured on maturing, or greyish); (38) margins pale green; (39) apices erose; (40) concealed or not concealed by overlapping awns. (41) Lower glume 2.2 to 5.5 mm long (average 3.8); (42) 4 to 9-nerved (frequently 4-7); (43) truncate to obtuse; (44) lanceolate to ovate. (45) Upper glume 2.8 to 6.3 mm long (average 4.0); (46) 3 to 7-nerved (frequently 5); (47) truncate to obtuse (rarely mucronate); (48) oblong to elliptic. (49) Body of the lowest lemma 2 to 3.3 mm long (average 2.7); (50) 1.4 to 2.9 mm wide (average 2.1); (51) apex truncate; (52) 9-nerved (rarely 10); (53) lacking extra nerves between main ones; (54) 1 nerve entering each peripheral awn; (55) surface deeply ribbed; (57) papillose; (58) yellow; (60) dorsally convex; (61) hairy on the lower part; (62) hairs as long as the body; (63) margins ciliate; (64) lacking marginal hyaline lobes. (65) Body width to the length 0.5 to 1 (average 0.8). (66) Body length to the length of the awns 0.4 to 1 (average 0.7). (67) Awns 9; (68) 2.1 to 8 mm long (average 5.1); (69) subequal; (70) bases lacking a thickened ridge; (71) yellow; (72) inner rim of cilia present. (73) Palea of the lowest floret 2.2 to 3.6 mm long (average 2.7); (74) hairy between the nerves; (75) apex cleft; (76) apex hairy; (77) hairy on the flaps. (78) Rachilla between lower two florets without a hair tuft. (79) Lemma of the second floret not ribbed; (80) glabrous. (81)

Anthers 0.8 to 2.1 mm long (average 1.3); (82) yellow. (83) Caryopsis 1.2 to 2.2 mm long (average 1.6); (84) 0.8 to 1.3 mm wide (average 1.0); (85) obovoid to ellipsoid. (86) Embryo 0.7 to 1 the caryopsis length (average 0.8); (87) 0.9 to 1.6 mm long (average 1.3).

Remarks: Burbidge (1941) included the material representing this species under *E. pallidus* and commented on the two forms, one with a loose panicle and the other with a dense panicle. The species differs from *E. pallidus* in the dense panicles that are more or less conical, and the deeply ribbed lemma; lateral branches interrupt the shape of the panicle especially in most of the Queensland material. Ewart and Davies' (1917) description of *P. nigricans* var. *compacta* appears to match *E. conicus*. However, as the present author did not see the type of var. *compacta* it was not possible to arrive at a firm conclusion about its status.

Distribution: Northern Territory, Queensland and Western Australia.
(Map 13a)

Ecology: The species occurs mainly in tropical and sub-tropical woodlands, brigalow forests, semi-arid shrub and low woodlands, *Acacia* shrublands and arid hummock grasslands (Moore 1970). Associated species include *Eucalyptus tessellaris*, *E. chloroclada*, *E. crebra*, *E. populnea*, *E. cambageana*, *E. argillacea*, *E. racemosa*, *Callitris columellaris*, *C. glauca*, *Angophora lanceolata*, *Cassinia laevis*, *Bauhinia* spp., *Acacia aneura*, thickets with *Brachychiton* sp., *Canthium oleifolium*, *Cymbopogon* sp., *Aristida armata*, *Bothriochloa decipiens*, *Eragrostis eriopoda*, *Chloris ventricosa*, and *Triodia* spp., etc. Soils range from white sands near the coast and river banks to yellow-brown sands, red to red-brown sandy loams, hard reddish lateritic to clay

loams.

Representative specimens (18/90)

NORTHERN TERRITORY: Old Coniston Homestead, Latz 1167 (CANB); 14 miles N. N. W of Alice Springs, Lazarides 5281 (BRI); 13 miles S. W of Yambah station, Lazarides 5188 (BRI CANB); south side of Mount Gillen, Pullen 10.468 (CANB); Pottoyu Hills, 55 miles S. E of Docker Settlement Latz 948 (CANB); Mallapunya Springs station, Latz 1531 (CANB); 15 miles S. E of Woodgreen Homestead, Nelson 2192 (AD CANB PERTH); Hamilton Downs station, Winkworth 298 (BRI).

QUEENSLAND: Agnes Lake, 79 km S. of Lyndhurst station, Simon & Clarkson 2747 (BRI); Brigalow Research Station, Johnson 2652 (BRI) 7 miles W. of Bauhinia Downs, Tothill H302 (BRI); Chinchilla, Hubbard & Winders 6435 (BRI); Gurulmundi, Belson BRI 286860 (BRI); 9 km S. W of Jericho, Beeston 1707C (BRI); Torrens creek, White 8747 (BRI); Prairie, Hubbard & Winders 7029 (BRI).

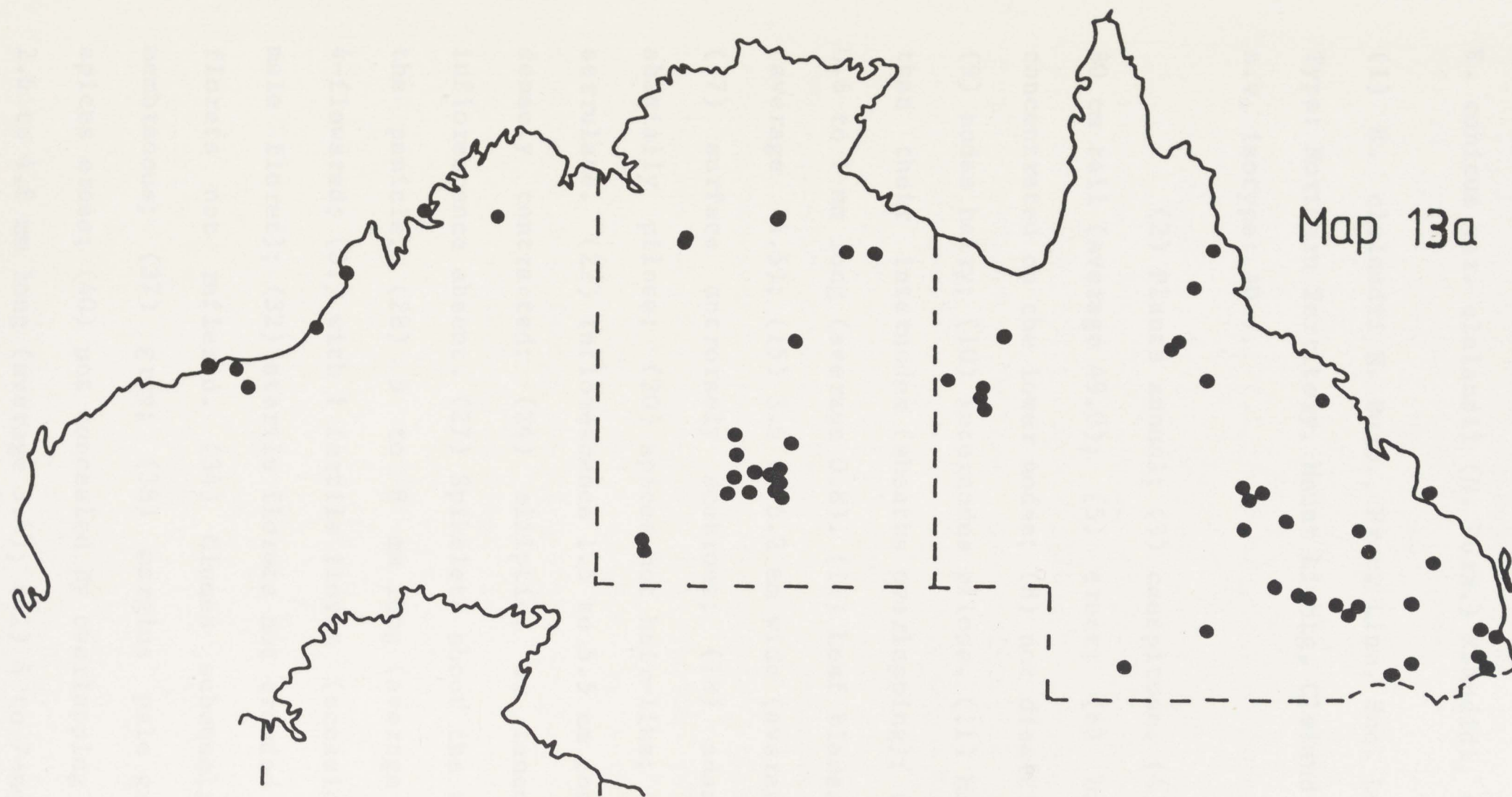
WESTERN AUSTRALIA: Rudall River, George 10653 (CANB); 86 km N. E of Sandfire road house, Beauglehole 59249 and Evrey 2949 (CANB).

References: Burbidge (1941: 79, with *E. pallidus*); Cameron (1979: 180, with *E. pallidus*); Cunningham et al. (1981: 96, fig. 20f); Gardner (1952: 37); Jacobs & Pickard (1981: 44); Lazarides (1970: 125, pl. 34b); Vickery (1953: 84); all as *E. pallidus*.

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Map 13a. Distribution of *E. conicus*.

Map 13b. Distribution of *E. conicus* var. *clelandii*.



Map 13a



Map 13b

5.8.20.1. Var. *clelandii*

E. conicus var. *clelandii* (N. Burb.) Kakudidi, stat. nov.

(1) *E. clelandii* N. Burb., Proc. Linn. Soc. Lond., 153: 80 (1941). -
Type: Northern Territory, Mount Liebig, Cleland L24. - Holotype: K,
n.v, isotype: AD !.

(2) Plants annual; (3) caespitose. (4) Flowering culms 31 to 80 cm tall (average 49.0); (5) erect; (6) branched; (7) branches concentrated on the lower nodes; (8) not disarticulating at the nodes; (9) nodes hairy; (10) internodes pilose. (11) Mid-culm sheaths longer than their internodes (sheaths overlapping); (12) hairy. (13) Ligule 0.6 to 1 mm long (average 0.8). (14) Leaf blades 7 to 20.7 cm long (average 14.5); (15) 3.6 to 6.2 mm wide (average 4.5); (16) involute; (17) surface antrorsely scabrous; (18) adaxially pilose; (19) abaxially pilose; (20) apices not hair-like; (21) margins antrorsely serrulate. (22) Inflorescence 1.5 to 5.5 cm long (average 2.8); (23) densely contracted; (24) elliptic, or lanceolate; (25) axillary inflorescence absent. (27) Spikelets about the same length throughout the panicle; (28) 5 to 8 mm long (average 6.7); (29) ovate; (30) 4-flowered; (31) with 1 fertile floret (occasionally with a second male floret); (32) sterile florets not crowded distally; (33) sterile florets not reflexed. (34) Glumes subequal; (35) pilose; (36) membranous; (37) grey; (38) margins pale green (to greyish); (39) apices erose; (40) not concealed by overlapping awns. (41) Lower glume 2.6 to 4.8 mm long (average 3.4); (42) 4 to 7-nerved (frequently 5-6); (43) truncate (rarely obtuse); (44) lanceolate to ovate. (45) Upper glume 3.1 to 4.8 mm long (average 4.1); (46) 4 to 6-nerved; (47)

truncate to obtuse; (48) oblong to elliptic. (49) Body of the lowest lemma 2.1 to 3.4 mm long (average 2.7); (50) 1.4 to 2.4 mm wide (average 2.2); (51) apex truncate; (52) 9-nerved; (53) lacking extra nerves between main ones; (54) 1 nerve entering each peripheral awn; (55) surface deeply ribbed; (58) yellow; (60) dorsally convex; (61) hairy on the lower part; (62) hairs as long as the body; (63) margins ciliate; (64) normally lacking marginal hyaline lobes. (65) Body width to the length 0.6 to 0.9 (average 0.7). (66) Body length to the length of the awns 0.5 to 0.9 (average 0.7). (67) Awns 9; (68) 2.4 to 5 mm long (average 4.0); (69) subequal; (70) bases lacking a thickened ridge; (71) grey; (72) inner rim of cilia present. (73) Palea of the lowest floret 2.5 to 3.2 mm long (average 2.8); (74) hairy between the nerves; (75) apex cleft; (76) apex hairy; (77) hairy on the flaps. (78) Rachilla between lower two florets without a hair tuft. (79) Lemma of the second floret not ribbed; (80) glabrous. (81) Anthers 0.8 to 1.4 mm long (average 0.9); (82) yellow. (83) Caryopsis 1.9 to 2.1 mm long (average 2.0); (84) 1 to 1.6 mm wide (average 1.1); (85) ellipsoid. (86) Embryo 0.8 to 0.9 the caryopsis length (average 0.82); (87) 1.5 to 1.8 mm long (average 1.6).

Affinities: This variety differs from the typical one by having greyish glumes and awns, and from *E. nigricans* in having shorter spikelets and membranous truncate glumes.

Distribution: Northern Territory. (Map 13b).

Ecology: The variety occurs mainly in *Acacia* shrublands and arid hummock grasslands (Moore 1970). Collector's notes include communities of dense shrubs of *Acacia* spp. and *Eucalyptus intertexa* on red loamy soils.

Representative specimens (7/10)

NORTHERN TERRITORY: Mount Liebig, 265 miles W. N. W of Alice Springs, Cleland L23, L24 (AD); Yuemdumu, Cleland AD 96244014 (AD); 1 mile W. of 16 mile bore, north to south stock route, Nelson 1735 (CANB); Haast's Bluff Reserve, Cleland AD 97215047 (AD); Haast's Bluff, 210 km W. N. W of Alice Springs, Cleland AD 96244033 (AD); Alice Springs, Sim AD 96803735 (AD).

References: Jessop (1981: 454); Lazarides (1970: 119), all as *E. clelandii* N. N. Burb.).

6. NATURAL HYBRIDS

Interspecific hybrids are rare in this group of species and only three based on morphological characters alone were recognised, namely *E. cylindricus* x *E. purpurascens*, *E. cylindricus* x *E. avenaceus*, and *E. polyphyllus* x *E. gracilis*. The plants examined were atypical, but possessed combinations of characters of their parental species. The presence of hybrids suggests that the parental plants are closely related, at least genetically if not morphologically.

6.1. *E. cylindricus* x *E. avenaceus*

In habit the plants resemble *E. cylindricus*, the flowering culms 24 to 50 cm high (more robust than *E. cylindricus*); erect; unbranched; disarticulating at the nodes; nodes hairy; internodes

hairy. Sheaths longer than their internodes; hairy. Ligule 0.6 to 1 mm long. Leaf blades 8 to 11 cm long (average 9.0); 2 to 3 mm wide (average 2.4); involute; antrorsely scabrous; adaxially and abaxially pilose; apices not hair-like; margins antrorsely serrulate.

Inflorescence 4.5 to 8.5 cm long (average 7.2); loosely contracted; linear; axillary inflorescence absent; spikelets about the same length throughout the panicle; 7.8 to 11 mm long (average 9.6); lanceolate; sterile florets not reflexed; not crowded distally. Glumes subequal; pilose; coriaceous; green; margins pale green; apices erose, or not erose; not concealed by overlapping awns. Lower glume 4.4 to 6 mm long (average 5.6); 9 to 12-nerved; obtuse to acute; lanceolate to ovate; upper glume 4.6 to 7.2 mm long (average 6.1); 7 to 11-nerved; truncate to obtuse (and erose); elliptic. Body of the lower lemma 2.9 to 3.2 mm long; 2.8 to 3.2 mm wide; apex truncate; 9 to 11-nerved; with extra nerves between the main ones; one nerve entering each peripheral awn; surface shallowly ribbed; papillose; yellow to grey; dorsally convex; hairy on the lower part; hairs longer than the body; margins smooth; lacking hyaline lobes; lemma body width to the length 1.0; the lemma body length to the awn length 0.4. Awns 9; 7 to 7.5 mm long; subequal; bases lacking a thickened ridge; grey to purplish; inner rim of cilia present. Palea 3.8 to 4 mm long; hairy all over between the nerves; apex cleft; hairy on the flaps. Rachilla with a hair tuft between the lower two florets. Lemma of the second floret not ribbed; hairy (readily glabrescent). Anthers 1 to 1.2 mm long, yellow.

Distribution: South Australia, 11.1 km N. of Lakes from Camp 1 on dunes in sandy swales, 28° 25.2' S 129° 40.5' E, Levitzke 77 (AD). Northern Territory, 24 km N. W of Indiana Homestead, Latz 1136 (BRI

CANB NSW).

6.2. *E. cylindricus* x *E. purpurascens*

In habit the plants resemble *E. cylindricus*; annuals; flowering culms 28 to 36 cm tall; erect; unbranched; disarticulating at nodes; nodes hairy; internodes pilose. Ligule 0.6 to 0.8 mm long. Leaf blades 8.9 to 12.5 cm long (average 9.9); 2.5 to 3 mm wide (average 2.8); involute; surface antrorsely scabrous; adaxially and abaxially pilose; apices not hair-like; margins antrorsely serrulate.

Inflorescence 9 to 13 cm long (average 10.5); loosely contracted; cylindrical; axillary inflorescence present; spikelets about the same length throughout the panicle; spikelets 7.4 to 9.8 mm long (average 8.4); lanceolate; 4-flowered; with 1 fertile floret per spikelet; sterile florets not crowded distally; not reflexed. Glumes subequal; pilose; coriaceous; green; margins pale green; apices not erose; not concealed by overlapping awns. Lower glume 5 to 6.2 mm long (average 5.6); 7 to 10-nerved; apex acute; lanceolate. Upper glume 5.1 to 7 mm long (average 6.3); 5 to 6-nerved; apex acute; elliptic. Body of the lowest lemma 3 to 3.4 mm long; 2.4 to 2.7 mm wide; 9-nerved; lacking extra nerves between the main ones; one nerve entering each peripheral awn; surface shallowly ribbed; papillose; yellow; dorsally convex; hairy on the lower part; the hairs longer than the body margins ciliate; lacking hyaline lobes; body width to the length 0.8; body length to the length of awns 0.6 to 0.8. Awns 9; 4 to 5.5 mm long; subequal; bases lacking a thickened ridge; purplish-pink; inner rim of cilia present. Palea 2.8 to 3 mm long; hairy between the

nerves; apex cleft; glabrous; hairy on the flaps. Rachilla with a hair tuft between the lower two florets. The lemma of the second floret not ribbed; glabrous. Anthers 1 to 1.2 mm long, yellow.

Distribution: Northern Territory, 2 miles E. of Quartz Hill, Latz 1122 (BRI).

6.3. *E. polyphyllus* x *E. gracilis*

In habit the plants are intermediate between the two species. Annuals; flowering culms 16 to 34 cm tall; erect to geniculately ascending; branched; not disarticulating at nodes; nodes hairy; internodes pilose; sheaths longer than their internodes; hairy. Ligule 0.4 to 0.6 mm long. Leaf blades 4.5 to 6 cm long; 2.4 to 2.9 mm wide; involute; surface antrorsely scabrous; adaxially and abaxially pilose; apices not hair-like; margins antrorsely serrulate.

Inflorescence 3.8 to 4.5 cm long; loosely contracted; elliptic; axillary inflorescence absent; spikelets about the same length throughout the panicle; 6.5 to 7.8 mm long; lanceolate; 4-flowered; with 1 fertile floret per spikelet; sterile florets not crowded distally; not reflexed. Glumes subequal; coriaceous; green; margins pale green; apices not erose; not concealed by overlapping awns. Lower glume 5.6 to 6 mm long; 10 to 13-nerved; acute; lanceolate. Upper glume 6 to 6.2 mm long; 6 to 8-nerved; acute; elliptic to lanceolate. Body of the lowest lemma 3.1 to 3.4 mm long (including 0.2-0.4 mm long callus); 2.8 to 3.2 mm wide; apex truncate; 9-nerved; lacking extra nerves between the main ones; with one nerve

entering each peripheral awn; surface ribbed on the upper part; yellow; dorsally convex; hairy on the lower part; the hairs longer than the body; margins smooth; lacking marginal hyaline lobes. Awns 4 to 4.4 mm long; subequal; bases with a slightly thickened ridge; yellow; inner rim of cilia present. Palea 2.8 to 3.4 mm long, hairy between nerves, apex cleft and hairy. Rachilla with a hair tuft between the lower two florets. Lemma of the second floret not ribbed; glabrous. Anthers 0.6 to 0.8 mm long; yellow. Caryopses 1.5 to 1.8 mm long; 1 to 1.2 mm wide; elliptic; embryo 0.7 the caryopsis length; embryo 1 to 1.2 mm long.

Distribution: Queensland, 23 miles W. of Camooweal, Chippendale 1489 (AD, BRI, CANB, NSW); common in heavy grey soils.

6.4 SIGNIFICANCE OF INTERSPECIFIC HYBRIDIZATION (see page 192b)

7. DISCUSSION

7.1. GENERIC DISTRIBUTION

Enneapogon is a tropical and sub-tropical genus and is known from the regions of Central and North America, Asia, northern, eastern and southern Africa and Australia. Members of the genus in Australia belong to the Gondwanan element in that the element results from the break-up of Gondwanaland. It has been pointed out that the genera belonging to this element have been on the continent since the time of its association with other parts of Gondwanaland, and so represent an ancient element of the flora (Clifford & Simon 1981). However, the

SIGNIFICANCE OF INTERSPECIFIC HYBRIDIZATION

Hybridization within species is widespread in nature and its contribution to variation in grass species is well recognized. Natural hybrids derived from local populations often present a complex array for systematics. The study of genome relationships in hybrids and some extensive biosystematic investigations have been helpful in classifying taxonomic relationships. However, the ease with which the species hybridize to produce viable F1 hybrids depends on a number of factors both internal and external, for example, seasonal isolation, gametic isolation, F1 hybrid sterility, etc.

In the genus *Enneapogon* the extent and significance of interspecific hybridization has not been worked out other than by recognition from the morphological characters. However, it is likely that these species share a common chromosome arrangement and, therefore, are close allies genetically. But judging from the relatively few (about 0.2% of the total specimens examined) that occur in the genus, their selection and stabilization must be a very rare event as interspecific hybrids are frequently subjected to high levels of gametic sterility.

Australian *Enneapogon* species do not occur in the other regions mentioned above where the genus occurs.

The distribution of *Enneapogon* in Australia as revealed by this study shows that the genus occurs over much of the continent but mainly in the drier regions of the interior. Climate plays a significant role in the distribution of plants throughout the continent and the distribution of *Enneapogon* in Australia can be related to the same. As revealed by this study the only species with a southerly extension of distribution is *E. nigricans* which extends into temperate northern Victoria and southeast of South Australia; there are no records from Tasmania. Burbidge (1941, 1960) was of the opinion that these areas are too damp and cold, and therefore the most plausible explanation for the absence of species of *Enneapogon* is geographic and climatic.

The correlation of this distribution to climatic factors appears as follows: Moore (1970) referring to the pastures pointed out that both heat waves and frosts can markedly influence both the seasonal growth pattern and the composition of the grassland communities. Much of Victoria, Tasmania and the southwest of Western Australia belong to the temperate zone. These areas have frost periods of 150 to 250+ days per year between mid-February and December which is of considerable importance ecologically. For example, *E. nigricans* has been noted for its ability to colonise and persist under harsh conditions and therefore its distribution would be expected to extend into these areas. However, Leigh and Mulham (1965) pointed out that the species is susceptible to frosts, which is the most plausible explanation for its limited distribution into temperate areas and also for the absence of other species. Thus it can be inferred that the

occurrence of *Enneapogon* southwards has been checked by prolonged frosts.

It is presently known that many of the tropical, sub-tropical and arid grasses are C4 plants and require high light intensities and temperatures for photosynthesis. The optimal temperatures for net photosynthesis in these grasses are around 35° C compared to 20° C for the temperate grasses (Langer 1979). While light intensity is rarely a major limiting factor at any season at any locality in Australia (Nix 1982), temperature seems to be of significant influence. As revealed by the present study *Enneapogon* occurs over much of the area with mid-summer temperatures exceeding 35° C; which suggests the high temperature requirement for net photosynthesis. Conversely, the greater part of the continent south of the Tropic of Capricorn has mid-winter temperatures falling below 7° C while the upland areas of New South Wales, Victoria and Tasmania have their July minimum temperatures falling to 2° C and below (Moore 1970); thus temperature rather than light becomes more influential. Related to low temperatures are the rainfall regimes of these areas. These areas are very moist and produce luxurious growth, which possibly results in high competition and a decrease in light availability for *Enneapogon* species that are adapted to the more open habitats of the Australian interior. Thus the genus is excluded from such habitats.

Northwards the genus *Enneapogon* crosses the Torres Strait into New Guinea in the Port Moresby region. As pointed out by Hoogland (1972) the similarity of the coastal habitats and the ecological conditions north and south of the strait would possibly account for such a distribution. Also it is believed that a land link existed between Australia and New Guinea (e.g. Burbidge 1960; Douth 1972;

Galloway & Loffler 1972; Galloway & Kemp 1981; Raven and Axelrod 1972) and because of the physiognomic and floristic resemblance of western Papua and northern Australia, several authors have treated Papua as part of the Australian floristic region (e.g. Good 1963). Webster and Streten (1972) expressed the opinion that the relationship between Australian and New Guinean floras must be treated on the basis of climatic history; during the last glacial maximum the exposed Torres land bridge and northern Australia would have been at least as arid as the Carpentaria region is today. The extrapolation of the vegetation types through the Quaternary by Nix & Kalma (1972) has suggested that the two regions shared a certain amount of flora. Therefore it would not be surprising for *Enneapogon* to have occurred over this region. That is, the genus existed north of the strait since the time of its association with northern Australia rather than being a recent migrant across the strait northwards. It is in a sense a relic of its former occurrence over the present Torres Strait, as the strait is considered to be much younger than the vegetation around it.

Barlow (1972) pointed out that there has been a fluctuation in areas of many species of Australian Loranaceae under the influence of variation in factors affecting their dispersability and habitat conditions. With regard to *Enneapogon* a similar situation affecting its occurrence appears to have taken place in New Guinea. As previously reported by Henty (1969) and also revealed by the present study, only two species, *E. pallidus* and *E. lindleyanus*, have their distribution extending to New Guinea in contrast to the majority of the species occurring in Australia. Presumably the species occurring on both sides of the strait have had access to similar suitable conditions for growth. However, the fluctuations in habitat conditions

north of the strait presumably led to its checked distribution northwards. While water and thermal regimes may be near optimal, the light regime is moderately limiting (Nix 1982). This is in agreement with what some collectors have noted regarding species distribution in New Guinea. It is apparent from such notes that light has become an influential factor within the region. For example, Pullen (6896 CANB) noted with regard to *E. lindleyanus* that the grass is dominant or locally common in small open patches in forests with poor soils but not seen elsewhere in the Port Moresby region. The low light intensities resulting from the luxurious forest vegetation, probably coupled with the the edaphic factor, have limited the generic distribution north of the strait. Conversely, it can be argued that the more or less cosmopolitan distribution in Australia is a clear indication that the habitat conditions have remained favourable south of the strait.

7.2. SPECIES DISTRIBUTION

The interpretation of the geographic distribution of the species in the Australian region is difficult because of the absence of sufficient information other than that available from the collectors' notes. In general terms *Enneapogon* species are widely distributed throughout the Australian interior in a wide range of vegetation communities and habitats. The species grow practically in all soil types including coastal sands, black clays and loams, light sandy loams and red-brown earths and sands. While it is rather difficult to correlate their distribution with soils, the most

plausible explanation for the present known distribution is that the apparent discontinuities of some species reflect a paucity of knowledge concerning the soils and plant life in the lesser known areas in Australia. Thus some species are limited to certain areas and others are more widely distributed, a feature common among Australian plants.

The distribution pattern, however, appears to match closely the principal floristic zones of the Australian region and the climatic zones, that is, the summer and winter systems of Burbidge (1960). Analysis of the species distribution in relation to her floristic zones shows that the majority of the species occur in the Eremaean zone, sometimes extending into the neighbouring interzones, while fewer occur in the tropical and temperate zones. There are no species limited to the temperate zone of the southeast, and none recorded from the southwest zone. Some species are abundant in the interzone 3, but decrease in abundance in interzones 1 and 2. *E. polyphyllus* has the widest distribution in that it occurs in all areas except the temperate zones, and *E. nigricans* has the most southerly distribution.

When distribution is correlated with rainfall, the pattern that emerges is that most taxa occur in the summer rainfall zone. However, *E. caerulescens* and its var. *occidentalis*, *E. cylindricus* and *E. nigricans* are mainly concentrated in the winter rainfall zone and extend slightly across the summer - winter isohyet of Burbidge (1960), while *E. polyphyllus* is more or less equally distributed north and south of the isohyet. While the rainfall system may be favourable for plant growth north and south of the isohyet, Nix (1982) pointed out that the radiation levels are substantially reduced in winter in

southern Australia due to the position of the sun and attenuation by the cloud cover. Related to that are the low winter temperatures south of the isohyet. Thus the low number of species concentrated in the winter rainfall zone appears understandable when the light requirement and the temperatures for maximum photosynthetic efficiency are considered.

While the Australian region does not have many marked topographical features, some mountain ranges within this region appear to have acted as refugia for some members of *Enneapogon*. Notable examples include *E. asperatus* in the Selwyn Ranges of western Queensland; *E. conicus* var. *clelandii* in the ranges of low mountains of central Australia; *E. eremophilus* in both the Selwyn Ranges and the ranges in central Australia; and a number of other species whose distribution is restricted to the region of the Dividing Ranges of eastern Australia. Apart from such refugia, *E. arenicola* is restricted to the coastal region of eastern Queensland and the nearby islands, while *E. pallidus* is restricted to the tropical zone of northern Australia extending from Western Australia through the Northern Territory to Queensland.

8. PHYLOGENY OF ENNEAPOGON

The taxonomic position of the tribe Pappophoreae to which *Enneapogon* belongs has been a source of disagreement and there are various opinions on the subject. With the exception of a few, the opinions have been largely based on comparative gross morphology. Attempts to classify the tribe have placed it in a number of

sub-families and tribes. For example, Bentham (1878) placed it in 'Primary series' (B) Poaceae under the tribe Astreptae as a sub-tribe Pappophoreae; Bor (1960) placed it in Pooideae; Parodi (1961), Stebbins and Crampton (1961), Reeder (1965), and Gould (1968) placed it in Eragrostoideae; Brown (1958) in the Chloridoid group; and Gould (1973) in the Festucoideae under the tribe Festuceae.

The morphological characters considered to be of taxonomic importance by many taxonomists with regard to the classification of sub-families and tribes are: number of perfect florets per spikelet; disarticulation of spikelets; position of reduced florets when present; and the shape of the lodicules. If these characters, that is, the presence of one or more perfect florets per spikelet; reduced florets above the perfect one; disarticulation of the spikelets above the glumes and the spikelets falling entire; are considered for *Enneapogon* then the genus is well placed in sub-family Festucoideae. The first three characters are in agreement with, for example, Gould's classification (1973). However, the short, cuneate lodicules compared with the Festucoideae type, which are elongated, pointed, thick at the base and membranous above, present some doubt on its position at the sub-family level.

If the leaf epidermal characters are considered, that is, the dumbbell- to cross-shaped silica cells; the presence of bicellular stalked-glandular hairs; triangular to tall, dome-shaped stomata; and the sinuous walls of long cells; then *Enneapogon* is well placed in the sub-family Panicoideae. However, the pattern of the costal zone, comprising single to double silica cells alternating with short cells, is not typical of the Panicoideae but similar to the Festucoideae.

A consideration of the internal leaf anatomy shows less of

the Festucoid features and more of the Chloridoid, Eragrostoid, and Panicoid features. Brown (1958) placed it in the Chloridoid group while Parodi (1961) and Reeder (1965), in combination with embryological characters, placed it in sub-family Eragrostoideae.

The results from cytological studies, that is, the small size of the chromosomes and the numbers, suggest that the closest affinities can be sought among the Chloridoideae, Eragrostoideae, and Panicoideae.

The relationship between *Enneapogon* and allied genera in the tribe Pappophoreae was discussed at length by Reeder (1965) on the basis of morphological, anatomical and embryological evidence. He expressed the opinion that *Enneapogon* is more closely related to *Cottea* and *Schmidtia* than to *Pappophorum*. The presence of hyaline lobes in *E. avenaceus* similar to those found in *Schmidtia* is a further confirmation of this relationship and probably a conservative feature in the Australian species.

The genus *Enneapogon* comprises about 30 species of which 20 are Australian. The Australian and the non-Australian species are comparable in many aspects and there is no doubt that they form a natural group. The Australian species, however, separate into two major groups on the basis of lemma features: those with a ribbed lemma of which *E. truncatus* is outstanding, and those with a smooth lemma represented by *E. avenaceus*. Intermediates between these groups occur. The non-Australian species appear to have characters of the first group. The ribbed lemmas of such species were observed by the present author in a few non-Australian species, and some are illustrated in various publications. For example, Beauvois (1812) and Gould (1973) illustrated *E. desvauxii*; Bor (1960) illustrated *E. elegans*, *E.*

brachystachyus, *E. persicus* and *E. cenchroides*. As Burbidge (1941) suggested, the ribbed lemma is probably less specialized, or the primitive feature; the species having it being more widely distributed and the smooth lemma being a more recently evolved character after the separation of Australia from other Gondwanan continents.

The number of nerves on the glumes is relatively many in the Australian species, that is, 4 to 21 (frequently 6 - 15) in contrast to 3 to 10 (frequently 3-7) in the non-Australian species (see "Taxonomic treatment" and Renvoize 1968). Numerous nerves on glumes is considered a less specialized character (e.g. Gould 1973), and the presence of such a state in the Australian species is an indication of the primitive nature of the group in this respect. Related to the nerves on the glumes are the nerves on the lemmas. In the Australian species the number exceeding 9 nerves is common, the extra nerves often ending blindly without extending into awns. Hence the following pattern of the broad outlines of the course of evolution of this genus: the earliest plants were characterized by broad numerous-nerved glumes - *E. avenaceus* being the outstanding relic in this respect; many-nerved ribbed lemmas as in *E. truncatus*; and each nerve entering a awn, that is, the trend having been directed at the reduction of the awns and nerves.

8.1. CONCLUSION

Depending upon the importance attached to the different characters used to classify the tribe and the genus, *Enneapogon* would appear to be related to different groups. The classification of the

genus and its allies would find closest affinities among the Panicoideae. A classification based on the leaf internal anatomy would find closest affinities among the Chloridoideae, Eragrostoideae and Panicoideae; while one based on gross morphology of the inflorescence and the spikelet would find its closest affinities among the Festucoideae. It is evident from the present study that it occupies a somewhat intermediate position between a number of large groups without being completely related to any one. Although an entirely natural classification has not yet been achieved, the tribes to which it seems most closely related are classified by authors like Stebbins (1956) Parodi (1961) and Jacques-Felix (1962) in the sub-family Eragrostoideae.

It can be assumed from the anatomical and morphological characters that evolution has not taken place at the same rate. In general terms cytology indicates that the genus, and especially the Australian species, has remained conservative. The evolutionary process that appears to have taken place in *Enneapogon* is that the inflorescence and the spikelet characters have evolved more slowly than the anatomical characters, which agrees with the opinions expressed by many taxonomists that the Festucoideae are a less specialized group.

As is true generally in biology, leaf anatomy is correlated with function, and function is associated with microscopic and submicroscopic structures. In grass leaf anatomy the arrangement of the tissues has been correlated with physiological processes of photosynthesis and starch accumulation. The physiological peculiarities and associated anatomical features are doubtless correlated with the distribution of grasses, so that the Panicoids,

Eragrostoids, Chloridoids and other related groups are tropical, sub-tropical and arid region grasses, while the Festucoids are temperate and cool region grasses (Hartley 1950). Thus, it can be inferred that the advancement of anatomical features in *Enneapogon* has evolved as an adaptation in a the harsh environment. The evolution of the Kranz syndrome adapted the plants to have maximum photosynthetic efficiency at the high temperatures and low water availability, which are features of the Australian interior where most species occur.

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